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THE *PINUS CONTORTA* VEGETATION OF
BANFF AND JASPER NATIONAL PARKS

by



ROGER JAMES HNATIUK

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled The *Pinus contorta* Vegetation of Banff and Jasper Parks submitted by Roger James Hnatiuk in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The *Pinus contorta* vegetation of Banff and Jasper National Parks was described and classified in relation to floristic composition, vegetation structure, and habitat. The historical development and successional status of certain sites was discussed.

The study consisted of two phases. (1) A Primary Survey in which 63 major sites (30 in Banff and 33 in Jasper) and 15 minor sites (13 in Banff and 2 in Jasper) were selected from studies of aerial photographs and from field observations. The Primary Survey involved a combination of plotless sampling techniques and phytosociological survey methods. A tentative classification was derived from the Primary Survey. Five sites representing different phases of the pine vegetation were selected for more intensive study. (2) The Intensive Study was done in a square, one hectare area subdivided into 400 contiguous 5 x 5 m quadrats. Information concerning plant species distribution patterns, plant species population structures, local topography, precipitation, and soil nutrient changes during the growing season were obtained from this study.

The classification presented consists of three Forest Classes--Moist, Mesic, and Xeric, which were subdivided into eight Forest Types--*Menziesia glabella* type, *Vaccinium scoparium* type, Feather Moss type, Mesic High Subalpine type, *Shepherdia canadensis* type, *Elymus innovatus* type, and *Arctostaphylos uva-ursi* type. The inter-relationships of

the stands of the Primary Survey as well as of the Forest Classes and Forest Types were analyzed by means of a Cluster Analysis. The results of the Cluster Analysis suggested a strong controlling influence of the water available to the plants and thus to the development of the various types of pine communities. The three Forest Classes were found to correlate well with elevation although a few exceptions did occur. The Moist Class predominated in the high subalpine zone, the Mesic Class in the mid subalpine zone, and the Xeric Class in the low subalpine and upper montane zone.

Pine Forests in the Mesic Class were rapidly being succeeded by *Picea-Abies* forests. Succession to *Picea-Abies* on mesic sites was described as slow, while on xeric sites succession to *Picea*, *Abies*, or *Pseudotsuga* was uncertain and appeared dependent upon an unusual juxtaposing of certain climatic conditions and availability of seed. Thus a physiographic pine climax exists on some xeric sites.

Distribution patterns of many plant species were correlated with local topography. In the case of some understory plants, their distributions were correlated with tree distribution patterns. No clear distinction was found in the pine vegetation between Banff and Jasper except that drier, warmer habitats were more extensive in Jasper than in Banff; therefore, the xerophytic and mesophytic vegetation types were more abundant in Jasper than Banff.

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I. SYSTEMATICS OF *PINUS CONTORTA*

Pinus contorta Douglas ex Loudon var. *latifolia* Engelmann ex Watson is a widespread species of western North America. It occurs in a variety of habitats, e.g. from just above sea level to over 11,000 ft. in the southern Sierra Nevada and Rocky Mountains and from the central Yukon to northern Baja California (Critchfield and Little, 1966). Lodgepole pine, as it is commonly known, has been described under several specific names since its published description 131 years ago by David Douglas. Synonyms for the species include *P. inops* (Bongard 1833), *P. banksiana* (Lindley and Gordon 1850), *P. murrayana* (Balfour 1853), *P. boursieri* (Carrière 1854), *P. bolanderi* (Parlatore 1868), *P. tamarac* (Murray 1869), and *P. tenuis* (Lemmon 1898). But the name *Pinus contorta*, given by Douglas in an 1838 publication describing his collections of 1825-26 on the coast of Oregon and Washington, has become the accepted name.

Critchfield in his 1957 monograph of the species has recognized four distinct geographic ecotypes on the basis of habitat, cone morphology, needle anatomy, and certain seedling characteristics. These groups he has called subspecies as follows:

- 1) *Pinus contorta* ssp. *contorta* - Pacific coastal group;
- 2) *Pinus contorta* ssp. *bolanderi* - Mendocino White Plains group, (California coast);

3) *Pinus contorta* ssp. *murrayana* - Sierra Nevada group;

4) *Pinus contorta* ssp. *latifolia* - Rocky Mountain group.

It is this latter group which occurs in Banff and Jasper National Parks.

Pinus contorta is known to hybridize with *P. banksiana* in northwestern Alberta (Moss 1949, Mirov 1956). According to cone characteristics described by Critchfield (1957) I think there is evidence of introgression of *P. banksiana* in Jasper and to a lesser degree in Banff. Such an hypothesis, though, requires detailed study into the extent and nature of hybridization between these two species before a definitive statement may be made.

II. OBJECTIVES

The objectives governing the field work for this thesis were:

(1) to describe the vegetation structure, floristic composition, and selected features of the physical habitat of forest communities dominated by *Pinus contorta* in Banff and Jasper National Parks;

(2) to relate variability in the communities to selected factors of the physical environment;

(3) to provide information of relevance to a larger study of the vegetation of the two parks being carried on by the Plant Ecology Laboratory of the Department of Botany of the University of Alberta. Some of the data gathered in this particular phase of the program, although not used in this thesis, may prove useful to future investigators (see Appendix 1).

In addition to the above points, the following objectives evolved later and were important in directing the development of the thesis:

(1) construction of a preliminary classification of the pine communities based upon vegetational criteria;

(2) the relationship of variability in the communities and features of their historical development and successional status.

III. PRIMARY SURVEY

A. SELECTION OF STANDS

Potential study sites were located from studies of aerial photographs (1:40,000, taken in 1949-1951), and from direct field observations. Most of the pine forests appear as smooth areas of grey on the photographs. In tone they usually appeared lighter than *Picea*, *Abies* and *Pseudotsuga* but darker than or the same as *Populus*. *Pinus contorta* could be distinguished from *Populus* primarily by texture - *Populus* having a "fluffy" (Raup and Denny 1950), "cotton-ball" appearance whereas the pine was either finer in texture or had conically-shaped crowns.

The pine forests were found in extensive tracts at middle altitudes over much of the major river valleys: the Athabasca, Sunwapta, and Bow (see Plate 1). They were also found, but of much lesser areal extent, in other river valleys as well as in isolated areas at high altitudes. The problem of delimiting stands within a seemingly continuous forest of pine was solved by using fire margins and topographic discontinuities as natural boundaries. These proved very adequate due to the rugged nature of the terrain, and the mosaic nature of even the major fires. These criteria proved to be valuable floristically in that the changes in the understory vegetation often accompanied topographic changes and to a lesser extent the age of the stand.

Because there was no dearth of sites to be studied,



Plate 1. Looking north up the Bow River Valley. The majority of the trees in the valley bottom, and on the lower and mid slopes are *Pinus contorta*. *Picea glauca* occurs immediately next to the river. *Picea engelmannii* and *Abies lasiocarpa* occur on the higher slopes (also the foreground trees).

sampling time was arranged so that a good geographic coverage of the two Parks was assured, with the exception of a few relatively small and difficult to reach areas in the upper Brazeau and Athabasca River Valleys, and the Blue Creek and Snake Indian Pass areas of northern Jasper Park. Sites were also selected to insure that the maximum range of elevations, slopes, and aspects were sampled. No attempt was made to obtain an unbiased estimate of the abundance of the pine forest types.

The selection criteria to be met in the field before a site was sampled were:

1. 75% or more of the basal area of the tree stratum had to be pine;
2. stand size had to be not less than approximately $\frac{1}{4} \times \frac{1}{4}$ mile (40 acres or *ca.* 16 hectares)
3. topography had to be uniform, in so far as mountain topography would allow, over the size of area being sampled (see below for discussion);
4. disturbance by man was to be minimal.

With reference to (3), it was impossible within the two Parks to apply a criterion of absolute uniformity. Uniform forests of pine originating from single fires often cover a wide range of topographic irregularity. Thus, smaller ridges, terraces, ravines etc. were often included within the area of a single stand (see p. 83) for discussion of the effect of this heterogeneity upon

the analysis of communities). Concerning (4), it was found that a criterion of absolutely no human disturbance would have eliminated vast areas of reasonably accessible forest. Man's presence in most areas was evident from the axe- or saw-felling of the occasional tree or sapling, by bits of old survey tape attached to trees or pegs, etc. Despite the subjective nature of (4), there was seldom any problem in deciding whether a site would or would not be studied on the basis of human disturbance.

B. SAMPLING PROCEDURE

Once a potential site was located, and a visual survey had been made along with an estimate of relative basal areas of the tree species (basal area being measured with a Bitterlich 10X prism at five points within the stand), the stand was then accepted or rejected from the study (by reference to the four selection criteria). If accepted, a four-hundred foot (*ca.*120m) base line was laid out in an east-west direction. Fifteen sampling points were located about this line as shown in Figure 1. The five points on either side of the line were located by pacing a random distance between 30 and 100 paces away from an perpendicular to it, using a table of random numbers. The minimum distance was used to prevent chance sampling of the same area twice (which would add little new information for the time and energy spent); the maximum distance was used to help reduce the chance of encompassing too

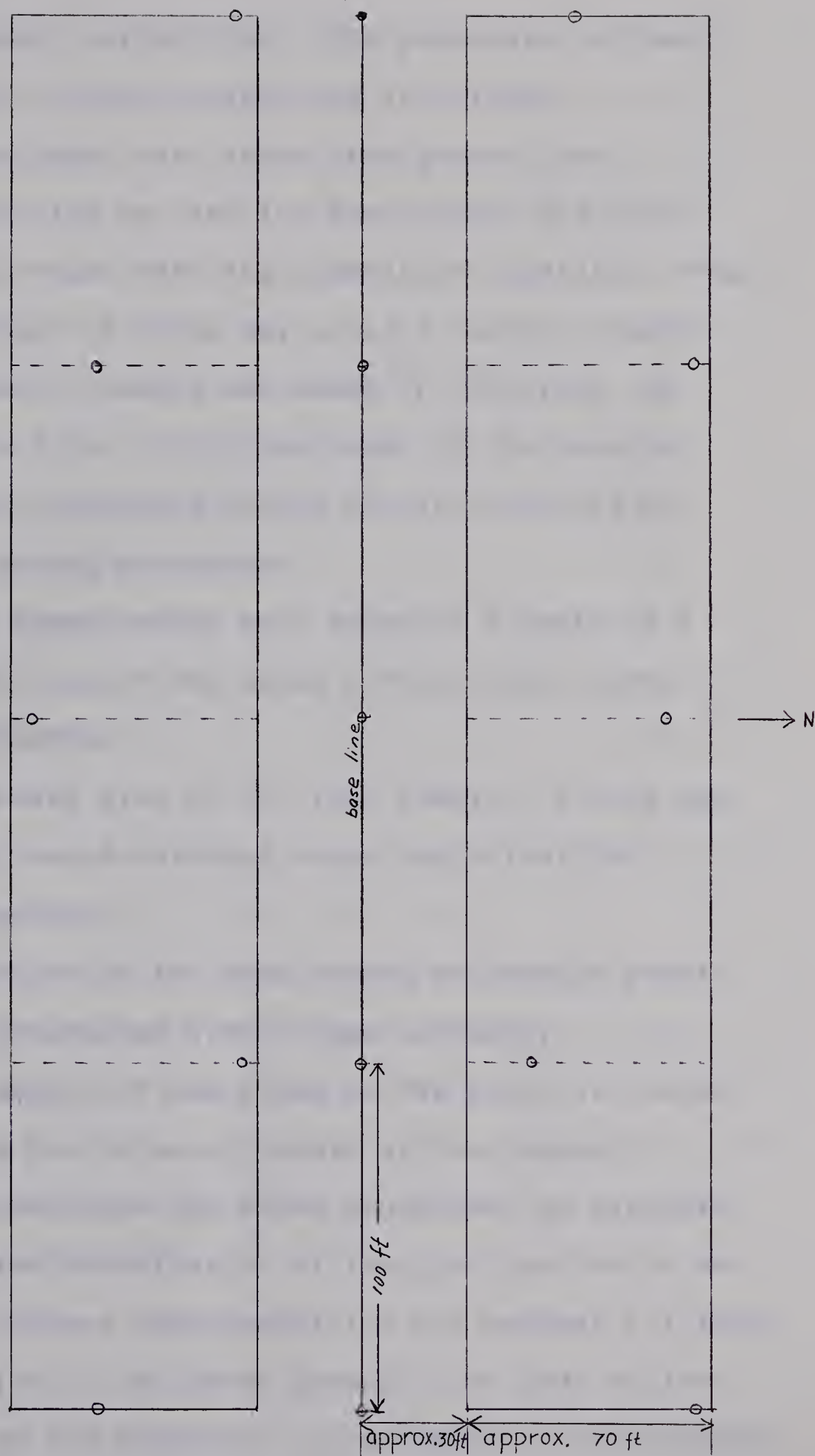


FIGURE 1.
Lay-out for the location of sampling points in stands of the Primary Survey.

much topographic variability. The procedure followed at each of the fifteen points was as follows:

1. Photographs were taken from ground level vertically up into the tree canopy and vertically down onto the understory vegetation from a height of about 2m, using a Yashica Ezmatic automatic camera and Kodak VP 126 black and white film. A list was made of the vascular plants occurring within the area covered by the ground photograph.
2. Soil temperatures were taken at a depth of 8 inches (*ca.* 20 cm) using a Weston dial probe thermometer.
3. The basal area of the tree species, living and dead, was determined using the Bitterlich 10X prism.
4. The slope of the area around the sample point was determined with a Haga altimeter.
5. The aspect of the slope at the point was noted using the 16 major points of the compass.

Having completed the above procedure, an estimate of the diameter distribution of the pine population was obtained by caliper measurement (to the nearest 0.1 inch at 4.5 feet [*ca.* 1.4 m] above ground, i.e. DBH) of 100 trees close to the baseline. An estimate of tree density was obtained by counting 200 living *P. contorta* trees (i.e. greater than 3 inches DBH) in a strip of land five or ten

yards wide (five yards for dense stands, ten yards for open stands) parallel to the base line. The distance travelled parallel to the baseline was noted for every 10 trees, and thus the total area occupied by the 200 living pine stems could be determined and density calculated. The number of dead trees, trees of other species, and stems less than 3 inches were also noted.

The age of the pine population was estimated by taking increment cores from one tree in each diameter size-class as follows:

1. for stands with a wide range of diameters, diameter-classes ran from 1-3 inches, 3-6 inches, 6-12 inches, etc. (ca. 2.5-7.5 cm, 7.5-15 cm, 23-30 cm).
2. for stands with a narrow range of diameters, one inch diameter-classes were used.

The largest pine tree found was also cored, as was the largest tree of any other species found in the stand. For each of the trees cored, an exact DBH was determined with a steel diameter tape. The height of the cored trees and the depth of their photosynthetic crowns were measured using a Haga altimeter.

A soil pit was dug at the 100 ft. point of the base line. Notes were made concerning the horizons found to a depth of 75 cm. Samples to be analyzed in the laboratory for mineral-nutrient content, texture, and water retention were collected from each of the horizons. In a few stands

with a greater than usual range of topographic heterogeneity, a second pit was dug in an area different from the first. Observations were made and samples were taken in a manner similar to the first.

A vegetation relevé was then compiled for the stand. It consisted of cover estimates of both feather mosses and of all vascular plant species found, as well as notes on vitality, sociability, and phenology (Table 1). Notes of a descriptive nature were made for each stand, including: general topography; amount and distribution of dead fall from the present stand and the previously existing stand; evidence of fire; evidence of animal trails, grazing and browsing; evidence of man's activities; the occurrence of *Arceuthobium americanum* (mistletoe) infection in the pine; and any other special features observed in the area studied.

Using the sampling procedure just outlined, 61 major sites were studied in 1966, 29 in Banff and 31 in Jasper. In addition, 10 "micro-stands" were studied in Banff. A "micro-stand" was defined as one which had some particularly interesting feature but which was unacceptable on the basis of the selection criteria or for which there was insufficient time to sample it completely (see Fig. 8 and 9 for locations of stands).

TABLE 1.

Phytosociological scales (J. Braun-Blanquet 1932
ex Stringer 1966)

Cover abundance:

- r - rare
- + - common, but cover less than 1%
- 1 - abundant, cover between 1 and 5%
- 2 - abundant, with cover between 5 and 15%
- 3 - abundant, with cover between 15 and 25%
- 4 - abundant, with cover between 25 and 50%
- 5 - abundant, with cover between 50 and 75%
- 6 - abundant, with cover between 75 and 100%

Vitality:

- 1 - well developed in stand, regularly completing life cycle;
- 2 - abundant and well established but usually not completing life cycle;
- 3 - scattered, and spreading only feebly or not at all, rarely completing life cycle;
- 4 - an unsuccessful adventive, occasionally germinating but not flowering or increasing vegetatively.

Sociability:

- 1 - growing as single distance individuals;
- 2 - growing in small groups or tufts;
- 3 - growing in patches or small cushions;
- 4 - growing in intensive patches or forming extensive carpets;
- 5 - growing in extensive masses, and as pure stands of wide extent.

Periodicity:

- fol - in foliage only
- fl - flowering
- fr - fruiting
- b - flower buds developed, but not yet opened
- sf - leafless.

The sampling procedure for the micro-stands consisted of (1) taking increment cores, height, and crown depth measurements from several representative trees of all species present (2) completing a relevé, including notes on features of interest, for the area.

During the summer of 1967, two additional major stands (one in each Park) and five micro-stands (three in Banff and two in Jasper) were studied, completing the Primary Survey.

IV. INTENSIVE STUDY

A. SELECTION OF STANDS

A preliminary study of the data from the 1966 primary survey showed that the pine vegetation could readily be divided into smaller communities on the basis of similarities and differences in physiognomy and floristics. The following tentative classification was constructed:

1. Stands with a conspicuous high shrub stratum

(a) Predominant shrub *Menziesia glabella* (41-B-I)¹

(Plate 2)

(b) Predominant shrub *Shepherdia canadensis*

(55-J-I)(Plate 3)

(c) Predominant shrub *Alnus crispa*

¹ The "I" after the stand number is used to distinguish the data of the Primary Survey from those of the intensive study of the same area. The "B" or "J" after a stand number indicates the Park in which the stand is located, i.e. Banff or Jasper respectively.



Plate 2. *Menziesia glabella* type. (41-B-I).

The shrub stratum is composed primarily of *Menziesia glabella* (blue green). *Shepherdia canadensis* is present (yellow green, left centre). *Picea engelmannii* can be seen in the tree stratum.



Plate 3. *Shepherdia canadensis* type (55-J-I).
Shepherdia canadensis is the only shrub to be
seen in this photograph. The herb stratum is here
dominated by *Elymus innovatus*. Feather mosses
are common in this area but form a thin carpet.

2. Stands lacking a high shrub stratum, but with a conspicuous low or dwarf-shrub stratum

(a) *Vaccinium scoparium* dominant (47-B-I) (Plate 4)

(b) *Arctostaphylos uva-ursi* dominant (24-J-I)

(Plate 5)

3. Stands lacking a conspicuous high, low, or dwarf-shrub stratum

(a) *Elymus innovatus* abundant

(b) Feather mosses abundant (*Pleurozium schreberi*,
Hylocomium splendens, *Ptilium crista-castrensis*)

(26-J-I) (Plate 6)

During the summer of 1967 it was possible to study five of the seven types listed above. These five are indicated in the above classification by the number of the stand sampled (i.e. the number of parentheses following the forest type). Because of the lack of time, stand 47-B-I was selected as a representative of both the *Vaccinium scoparium* and *Shepherdia canadensis* types in Banff.

B. SAMPLING PROCEDURE

The sampling plan for the intensively studied forests was completely different from that used in the primary survey. A square area of one hectare (i.e. 100 x 100 meters) was established in the study area and subdivided into 400 5x5 m quadrats (Figure 2). A Brunton transit was used in marking out the area in a grid form with the major axes lying in a north-south and an east-west direction.

THE UNIVERSITY OF CHICAGO

CHICAGO, ILLINOIS 60637

TO THE PRESIDENT OF THE UNIVERSITY OF CHICAGO

FROM THE DEAN OF THE FACULTY

SIR:

I have the honor to acknowledge the receipt of your letter of the 10th inst.

concerning the

appointment of a

member of the Faculty of the University of Chicago.

I am sorry to hear that you are unable to accept the offer.

Very respectfully,

Yours very truly,

THE PRESIDENT OF THE UNIVERSITY OF CHICAGO

THE DEAN OF THE FACULTY

THE UNIVERSITY OF CHICAGO

CHICAGO, ILLINOIS 60637

THE PRESIDENT OF THE UNIVERSITY OF CHICAGO

THE DEAN OF THE FACULTY

Very truly yours,

THE PRESIDENT OF THE UNIVERSITY OF CHICAGO

THE DEAN OF THE FACULTY

THE UNIVERSITY OF CHICAGO

CHICAGO, ILLINOIS 60637

THE PRESIDENT OF THE UNIVERSITY OF CHICAGO

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Plate 4. *Vaccinium scoparium* type (47-B-I).

Vaccinium scoparium forms a nearly continuous dwarf shrub stratum. Feather mosses and *Cladonia* spp. form a stratum below the *Vaccinium*. *Arnica cordifolia*, and *Elymus innovatus* can be seen in the plate.

Decomposing logs of trees of the previous forest, litter the ground.



There is a great deal of interest in the
subject of the history of the
people of the world, and it is
very interesting to see how
the different nations have
developed and changed over
the years. The study of
history is a very important
part of our education, and
it helps us to understand
the world around us.



Plate 5. *Arctostaphylos uva-ursi* type (24-J-I). The very low dwarf shrub stratum is dominated by *Arctostaphylos uva-ursi*. A *Juniperus communis* plant can be seen to the right of centre. Isolated shrubs such as this are typical of the type. A small amount of *Elymus innovatus* can be seen in the background. *Linnaea borealis* is more common in the denser area of pines (centre right).

Note the bare ground in the centre foreground and the rings of *Arctostaphylos uva-ursi* at the base of the pine trees. The bare ground appears to be the result of trampling caused by the numerous elk which feed in the area.



Plate 6. Feather Moss type (26-J-I).

Pleurozium schreberi is abundant in the open area (centre). *Hylocomium splendens* is abundant in the moister, more shaded area beneath *Picea mariana* (lower, right foreground). Abundant *Picea mariana* reproduction, mostly from layering, is evident. Numerous fallen trees from the present forest can be seen. These fallen trees are slow to decay if they are not in direct contact with the ground.

Quadrats were flagged at their corners.

Within the grid area (the "stand") the following observations were made:

1. For all quadrats

(a) Density of all tree species

The number of trees in each quadrat were noted by species and by three inch diameter-classes at breast height. The numbers of seedlings, transgressives, and saplings for each species were also tallied per quadrat.

Size classes were defined as follows:

Seedlings - individuals less than 12 inches
(30 cm) tall;

Transgressives - individuals greater than
12 inches tall but less than
1 inch (2.5 cm) in DBH;

Saplings - individuals with a DBH between
1 and 3 inches (7.5 cm);

Trees - individuals with a DBH greater than
3 inches;

(b) Cover and Frequency

(i) The frequency of occurrence on a per quadrat basis of all vascular and certain non-vascular plants was noted by recording a subjective estimate of cover¹ for

¹ Cover scale used was the same as that for the relevés in the Primary Survey (see Table 1).

each species.

(ii) A vertical, overhead, point-sampling device (constructed in the Plant Ecology Laboratory, University of Alberta, by Messrs. Laidlaw and Hnatiuk) was used to point-sample the cover of the tree stratum over the corners of the quadrats.

(iii) Exposure of quadrat corners to the sky was estimated by means of a Lemon Model a convex Forest Densiometer.

(c) Local topography

(i) Data for the construction of a map of the local topography of the stand were obtained by measuring the slope of the land between the corners of each quadrat with a Haga altimeter.

(ii) General notes on micro-relief within the quadrat (e.g. hummocks) were taken.

(d) Soil temperature

Soil temperatures at a depth of 20 cm were taken at the quadrat corners.

(e) Soil samples

A soil pit was dug at a depth of 75 cm in one randomly selected quadrat. The soil profile was described and samples were collected from each horizon for laboratory analysis.

2. For twenty-five selected quadrats:

The grid was partitioned into 25 20x20 m blocks, each containing 16 quadrats. Using a random numbers table, one of the 16 quadrats in each block was selected for more intensive study as outlined below.

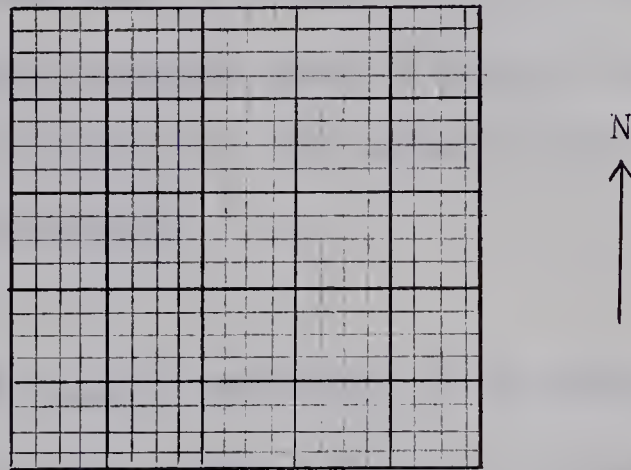


Figure 2. Layout of Intensive Stand Showing Quadrats and Blocks of Quadrats

(a) Point-cover

Four east-west lines were positioned at random distances from one corner of the quadrat.

Twenty-five randomly selected points were sampled along each of the lines by lowering a No. 14 (British) knitting needle vertically to the ground over the point and recording by species the plants touched by the needle.

(b) Density and diameter distribution of tree populations

The DBH's of individuals of all tree species were measured with Swedish tree calipers.

(c) Tree age, height and crown depth

Using the lines used in point-cover determination, a random point was chosen. The tree

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(not necessarily in quadrat) nearest that point was cored at breast height to determine its age and was measured for height and crown depth.

(d) Tree basal area

A basal area reading of trees having a diameter at breast height greater than 3 inches was taken using a Bitterlich 10X prism at the center of the quadrat.

(e) Soil

A surface soil sample (maximum 30 cm where possible) was taken using a one inch-diameter soil auger. Because of the extreme stoniness of most of the soils, the depth of auger penetration was limited and variable. Within the quadrat several samples were taken, depths recorded, and samples pooled as a representative sample of the surface soil.

(f) Non-vascular plant sample

Because of the investigator's limited knowledge of the non-vascular flora, a mass collection of bryophytes and lichens was made from a randomly chosen 25x25 cm square area in each quadrat and stored in a labelled paper bag for future identification.

(g) Vegetation relevé

A relevé of the same type used in the primary

survey (p. 11) was completed for the quadrat.

(h) Photographic records

- (i) The ground vegetation in the centre of quadrat was photographed in a manner similar to that used in the Primary Survey.
- (ii) From ground level over the centre of the quadrat a photograph was taken vertically up into the canopy. The photograph was to be used in the determination of exposure of the point to the sky.
- (iii) A colour photograph of a lateral view of the quadrat was taken using an Asahi Pentax SLR 35 mm camera and a 55 mm lens.

(i) General Notes

General notes were taken concerning the relationship of the quadrat to the surrounding stand as well as special features noted within the quadrat.

- 3. A vegetation relevé including general notes was made for the stand as a whole.

V. PRECIPITATION AND SOIL-NUTRIENT SURVEY: SUMMER 1968

The two main objectives of the field work during the summer of 1968 were to study (1) precipitation differences between the five intensive sites and (2) the fluctuation in available soil nutrients through the growing season in the same five sites.

A. PRECIPITATION

It became evident during the summers of 1966 and 1967 that precipitation patterns in the mountains were very complex due to the large scale irregularity of the landscape. The topography of Banff Park is dominated by the glaciated Bow River Valley which is rimmed by high mountains (9,000-10,000 feet). Cutting through the mountains from the west and opening into the Bow Valley are several smaller valleys (e.g. the Redearth, Altrude, and Bath Creek Valleys). During the summer at least, rain storms appear to come predominantly from the west. The storms tend to come into the Bow Valley via the small side valleys. This means that both the small side valleys and the adjacent areas of the Bow Valley receive frequent rain whereas a rainshadow is present on the east-facing slopes of the Bow Valley between the mouths of the side valleys. The situation on the west-facing slopes of the Bow Valley is more complex. Storms moving out of the small valleys to the west may move directly across the Bow Valley and over its eastern wall, releasing rain as they pass. Alternatively the storms may be deflected up or down the main valley or move out via small valleys on the east side of the Bow Valley.

A similar situation exists in Jasper where the Athabasca and Sunwapta River Valleys are the counterparts of the Bow Valley in Banff. Primary side valleys coming from the west in Jasper are the Whirlpool and Miette River Valleys and the Snake Indian and Snaring River Valleys from the northwest.

Thus it can be seen that precipitation records from one place may not be applicable to another place only a mile or so away.

The following procedure was used to measure precipitation at each of the five sites during the period of observation. From three to five 48 oz. tins were set out in each of the intensive stands during the last week of May. Where possible, the tins were placed beneath openings in the tree and shrub strata. A layer of heavy mineral oil was poured into each tin to reduce evaporation loss. Although several of the tins were tipped over during the summer, some indication of precipitation received at the floor of the stand was obtained. Only minimum precipitation data (i.e. the tins were full) were obtained from stands 47-B-I and 55-J-I due to the very high precipitation received by these areas. A larger totalizing rain gauge was set in the largest open area near each stand. Each gauge consisted of a buried two-gallon (ca. 9 liters) storage container (with a layer of heavy oil) connected to a receiver (approximately 10 cm square) about 20 cm above the ground. The base of the receiver was surrounded by a layer of feather mosses to prevent rain from splashing into the receiver.

Difficulty was experienced in locating these gauges in open areas and yet preventing their being disassembled by park visitors and/or wildlife. At the first summer check only one gauge was intact (24-J-I), but at the fall determination only one of the gauges had been visibly tampered with.

B. SOIL NUTRIENTS

Using markers set up the previous year, the exact location of the stand was found. At each of five widely-spaced points within the stand, soil samples were collected from two horizons (0-15 cm and 15-30 cm) at the end of May, in early August, and early September. Each sample consisted of pooled collections from three pits dug within a 5x5 m area. The 2 mm fractions of these samples were subsequently analyzed for N, P, K, pH, conductivity, and free lime by the Agricultural Soil and Feed Testing Laboratory in Edmonton.

VI. LABORATORY ANALYSIS OF SOILS

A. CHEMICAL ANALYSIS

Chemical analysis of the less than 2 mm fraction of the soil and humus was carried out by the Agricultural Soil and Feed Testing Laboratory in Edmonton. The analysis included:

1. Available nitrogen (lbs per acre)
2. Available phosphorous (lbs per acre)
3. Available potassium (lbs per acre)
4. pH
5. conductivity (mmhos)
6. Semiquantitative estimates of:
 - (a) sodium
 - (b) organic matter
 - (c) free lime (CaCO_3)

B. PHYSICAL ANALYSIS

The following analyses were made on the less than 2mm

fraction of the soil sample:

1. Particle size distribution

The percentage weight of the sand, silt, and clay particle size-classes (U.S.D.A. classification) were determined by the Bouyoucos method (see Appendix 2 for modifications).

2. Soil water retention properties

- (a) Field Capacity (FC) was determined using a 1/3 atmosphere, porous, ceramic-plate pressure-extraction apparatus (Soil Moisture 3-Bar Extractor #1600).

- (b) Permanent Wilting Percentage (PWP) was determined using similar apparatus at 15 atmospheres (Soil Moisture 15-Bar Extractor #1500).

- (c) Available Water was taken as the difference between Field Capacity and Permanent Wilting Percentage.

All calculations were based upon the average of duplicate samples which differed from one another by not more than 1.5%.

VII. NUMERICAL CLASSIFICATION METHODS

One of the major problems in the quantitative approach to synecology is to find methods which permit the analysis and synthesis of large quantities of data in a period of time justifiable by the anticipated results. Numerous techniques have been developed which solve this problem to

some extent, and it is not my intent to provide a complete comparative analysis of these in relation to the ones used. Comments will be limited to the advantages or disadvantages of the methods used.

A data-grouping technique was sought which would (1) elucidate discrete or nodal taxa, (2) indicate the relationships between taxa and between individual units within a taxon. The individual units were the stands of the primary survey. The numerical classification was attempted to see whether semi-quantitative vegetation data from a primary survey could be used to develop an objective and ecologically meaningful classification of the pine vegetation which could be related to a classification based upon subjective criteria.

A. FACTOR ANALYSIS

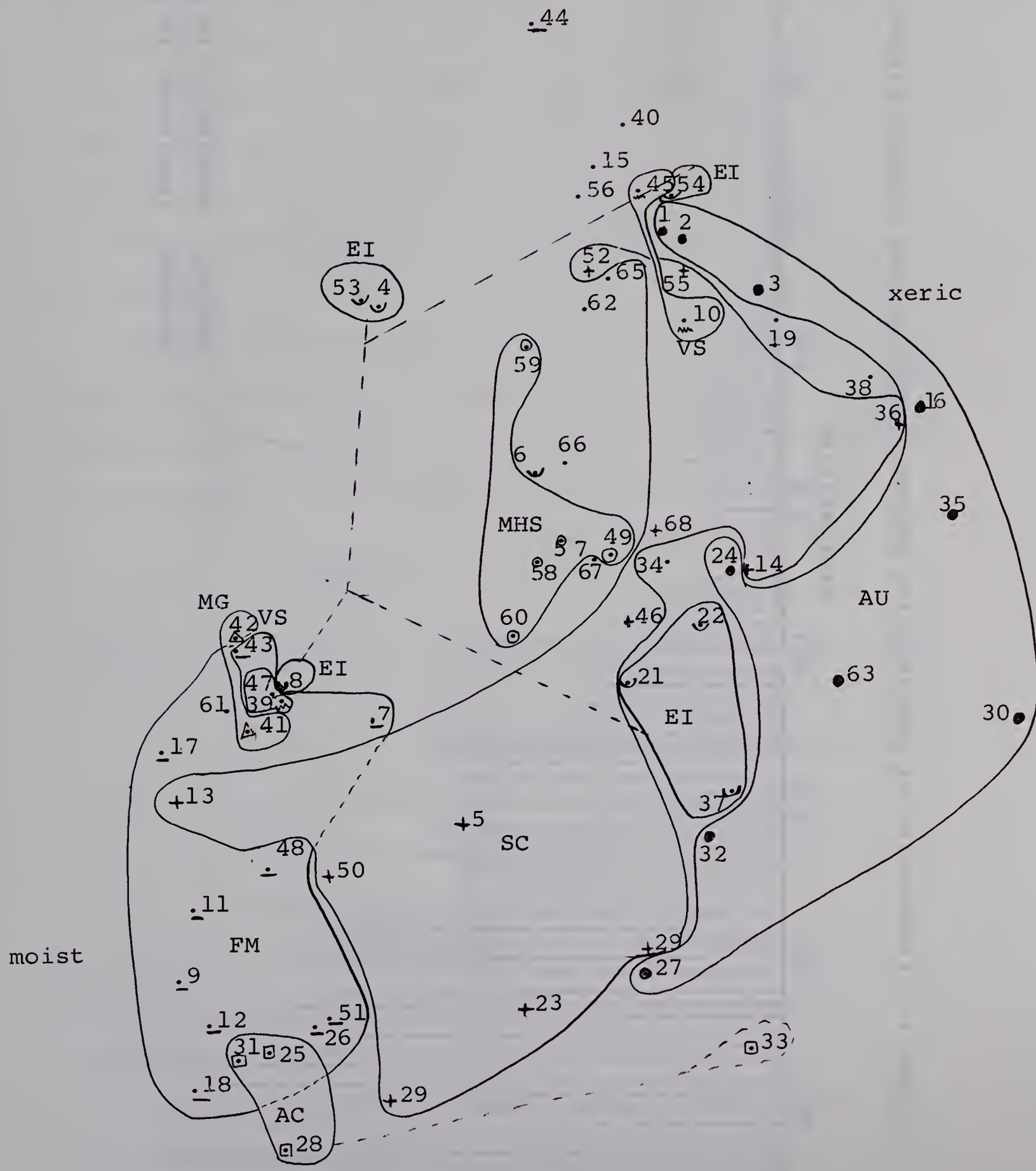
A principal components technique of factor analysis (program from the Division of Educational Research Services, University of Alberta) was attempted using the species-cover data for the primary survey stands. Twelve statistically significant factors were indicated by the analysis but the stand groupings were very indistinct. The patterns appeared to be too complex to justify detailed work considering the limited information available about each stand. In addition to this there were technical problems in finding computer programs which could handle the large data sets being used.

B. ORDINATION

Several attempts were made to utilize ordination methods (after Orloci 1966) in synthesizing the raw data to a more usable form. When the cover of feather mosses was included in the data input to the ordination, a large but fairly distinct group of stands was isolated from a diffuse scattering of other stands in a two dimensional view of the ordination field. The result (Figure 3) could be interpreted in terms of a moisture gradient. But because the moisture status of a site is determined by several factors such as altitude, local precipitation patterns, soil texture, ground water drainage, etc., stands which were ecologically distinct tended to be grouped into a single unit. Stand distribution on the ordination changed drastically and unpredictably each time a new view of the ordination was constructed using a different set of axes. When Pearson's Correlation Coefficient was calculated between the coefficient of dissimilarity of stand pairs and their two-dimensional separation on the ordination, the "r" values ranged between 0.2 and 0.5. The average Index of Similarity between stands was 0.24. The general dissimilarity between stands is further emphasized by the histogram of these indices (Figure 4). In view of the low "r" values and the low average similarity of the stands, it seems reasonable that the ordinations in two dimensions accounted for very little of the variation present in the data. Because of the drawbacks just noted, an ordination

FIGURE 3. ORDINATION OF STANDS OF PRIMARY SURVEY (METHOD OF ORLOCI 1966), end stands: 22 - 61, and 15.

Feather Moss type \pm
Alnus crispa type \square
Vaccinium scoparium type \sim
Menziesia glabella type \triangle
Shepherdia canadensis type $+$
Elymus innovatus type \smile
Arctostaphylos uva-ursi type \bullet



-average similarity is 0.24
-median similarity is 0.11

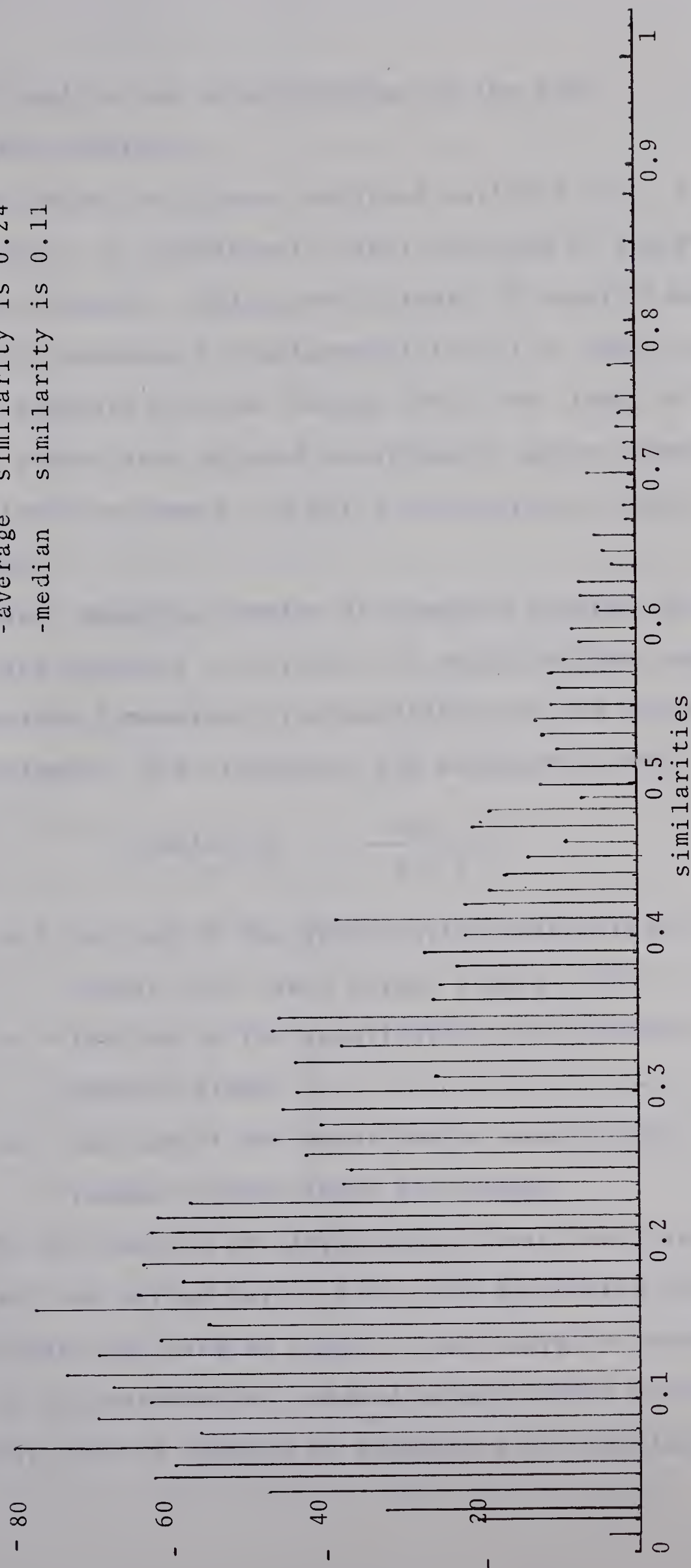


FIGURE 4. Frequencies of Similarities between Stands of the Primary Survey

was not used in the interpretation of the data.

C. CLUSTER ANALYSIS

The method of cluster analysis outlined by J. A. George and J. W. Carmichael (1966) was used in the process of data synthesis. Using coefficients of vegetational similarity proposed by Czekanowski (1913) as input to the cluster analysis program (George 1966) the stands of the Primary Survey were grouped according to gross vegetational similarities (see p. 43 for a discussion of these groupings).

Ream's modified Fortran IV computer program (Wisconsin 1962) (see Appendix 3 for list of modifications) was used to calculate a numerical representation of the similarity of two stands. The similarity was calculated thus:

$$\text{similarity} = \frac{2w}{a + b}$$

where: a = the sum of the quantitative observations of one stand, (i.e. cover values (see p. 247)

b = the sum of the quantitative observations of another stand;

w = the sum of the quantitative observations in common between these two stands.

The half matrix of similarities (less the diagonal elements) was sorted into a series of decreasing similarity values which was used as input to the George's program.

The cluster analysis method groups stands into "clusters" and is capable of indicating the distinctness of

these clusters as well as how they are related to other clusters and individual isolated stands. The program groups the data at many levels of similarity. The highest levels indicate the most distinct clusters, while the lower levels result in clusters formed under less stringent criteria. These levels of resolution are analagous to levels of a hierarchical classification.

To illustrate the results of the clustering process more clearly, the following description is given. It is based upon the cluster analysis used in this thesis. At the highest levels of resolution, only stands which are very similar to one another are included in the same cluster. Clusters such as these are indicated in Figure 5 by a dashed line. At the next lower level of resolution it can be seen that several of these clusters are brought together into a single cluster while other clusters of the previous level remain independent. Similarly in the other two levels shown, larger and larger clusters are formed. At each level of resolution, linkages (i.e. similarities) between groups or between individual stands and groups are indicated. These are shown in Figure 5 by dotted lines.

As the level of resolution drops, the trend of the synthesis is to bring together into one cluster, stands which are less and less similar. Thus at lower levels of resolution, stands which may be transitional between major clusters become incorporated into one of these clusters.

The value of the cluster analysis, therefore, lies in its capacity to indicate major units or "clusters". Clusters

of points may be defined as those in which the "average within-cluster similarities are high compared to the between-cluster similarities" (George and Carmichael p. 13). The results of the analysis are not as refined as those of factor analysis but they are valuable when used in the synthesis of preliminary survey data of the type used in this thesis.

The cluster method assumes that if there are any clusters in a set of data, then surely the most similar pair of stands will be a member of one of these clusters and thus form the starting point of the synthesis. The stand with the highest similarity with any stand already in the cluster is then chosen and subjected to the following tests before being admitted to the cluster:

1. Average linkage criterion

The difference between the average linkage (i.e. similarity) of all points in the cluster before and after the prospective point is added must not exceed a specified level. This level of acceptance is increased at each level of resolution. Thus a sudden drop in the average linkage of a cluster when a new point is added indicates that that point is separated from the main cluster by a relatively large "open space" and therefore is not a member of the cluster. In general, as each cluster is completed and as long as stands are still not members of clusters an attempt is made

to form new clusters with the remaining stands.

2. Single linkage criterion

This test compares the average of all single links (i.e. the average of the single similarities by which each stand was selected for admittance to the cluster) within the cluster to the single link which would bring the prospective point into the cluster. If the difference is too great then the point is not admitted. Again the maximum acceptable difference is arbitrarily set low at the first level of resolution and increased at each subsequent level in the clustering process.

3. Ratio criterion

This criterion, which we call the "ratio criterion" was based on the following rationale: if the rank of the similarities, during the growth of a cluster, dictates that the cluster become large in some dimension(s) before considering points for admission, then intuitively these points should be denied admittance until a low level of resolution.

(George and Carmichael 1966, p.43-44)

4. "Not-in-a-cluster" criterion

If the prospective point has already been admitted to another cluster, then it cannot be admitted to a second cluster at the same level of resolution.

The summarized result of the cluster analysis can be seen in the discussion of communities (p. 43). This form of analysis permits the description of particular

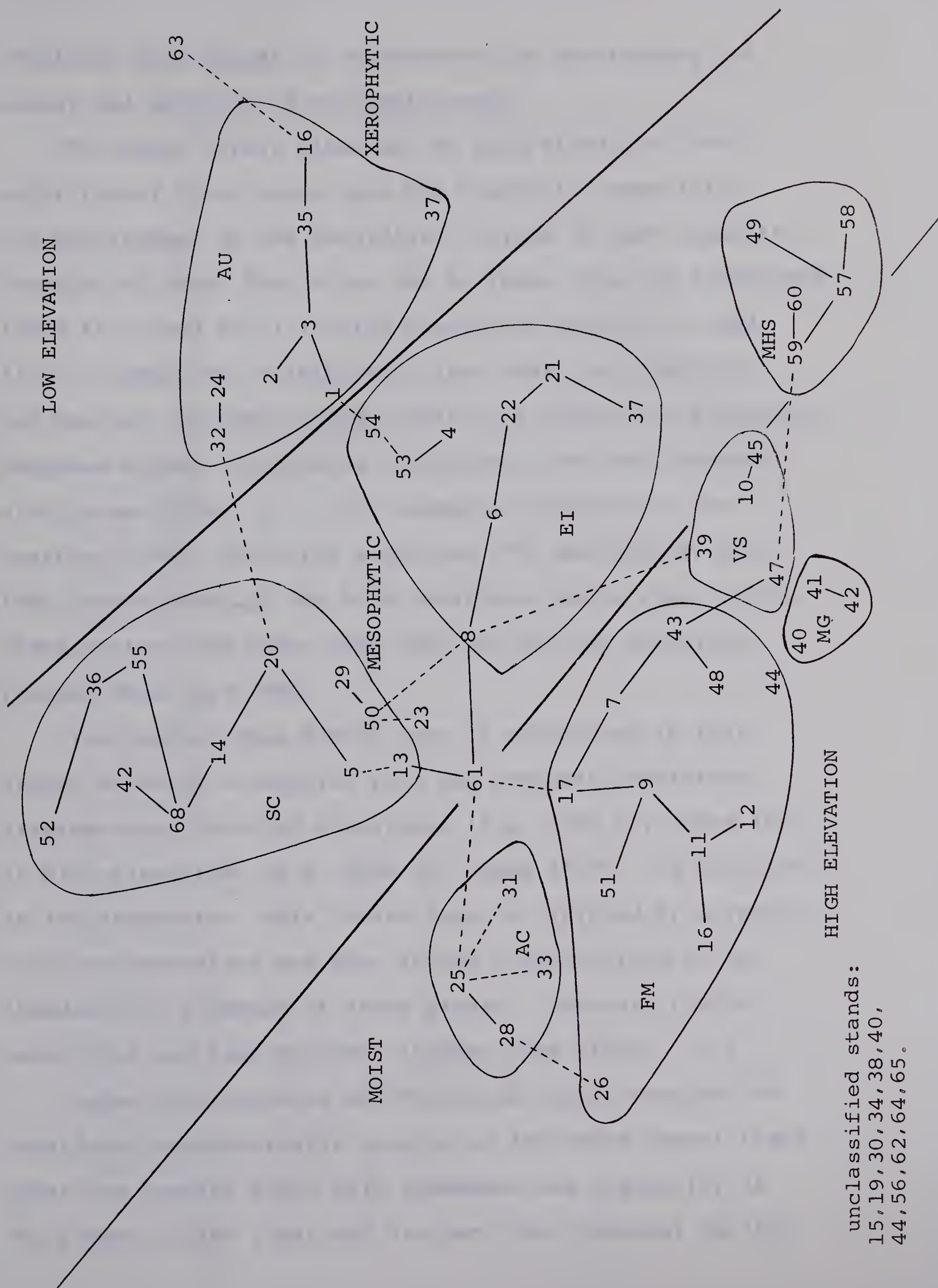
types of communities characterized by certain attributes. The recognition of discrete community types is extremely useful ecologically, even if it is recognized that the clusters are arbitrarily delineated in a reality where gradients occur from one such classification unit to another.

The technique of cluster analysis is also useful in that it indicates relationships between some of the clusters it identifies in a set of data. This is accomplished by "looking" at the clusters from increasingly greater "distances", i.e. levels of resolution. (Figure 6). Thus, small clusters are linked to larger clusters and isolated individuals become more closely associated with certain clusters. The result is an integrated view of stand relationships.

VIII. DESCRIPTION OF FOREST TYPES

The *Pinus contorta* vegetation of Banff and Jasper Parks can be divided into three main classes on the basis of moisture available to the plants. The three classes - Moist, Mesophytic and Xerophytic - were subjectively determined from the floristic composition and lushness of growth of the plants in each stand. The geographic distribution of these kinds of forests is controlled by factors such as elevation, slope, aspect, and position relative to mountains and valleys. Each of these factors affects local precipitation and soil-water drainage patterns. Soil texture and

FIGURE 6. CLUSTER ANALYSIS OF STANDS OF PRIMARY SURVEY. 39



stoniness also appear to be important in determining the amount and duration of available water.

The Moist Forest Class may be subdivided into four major forest types based upon the floristic composition and physiognomy of the subordinate strata in each community. Examples of these four types can be found from low elevations (3700 ft. stand 26-J) to high elevations (6100 ft. stand 41-B). Therefore, within this class there are floristic and species-abundance changes which are related to elevation. *Empetrum nigrum*, *Lycopodium complanatum*, and *Rhododendron albiflorum* (Table 2), for example, characterize the *Menziesia* (MG), *Vaccinium scoparium* (VS) and Feather moss (FM) forest types of the high subalpine, while *Alnus crispa* characterizes the *Alnus* type (AC) and the low elevation Feather Moss type (FM).

The Feather Moss forest type is ubiquitous in that stands in which bryophytes form the dominant understory stratum occur from low elevations (e.g. 3,700 ft, stand 26-J) to high elevations (e.g. 6,000 ft. stand 48-B). In addition to the bryophytes, this forest type is typified by a sparse vascular understory and thus is not characterized by the abundance or presence of other plants. However, *Pyrola asarifolia* has high presence in this type (Table 2).

Ledum groenlandicum and *Vaccinium caespitosum* may be considered characteristic species of the Moist Forest Class. These two species occur with abundance and regularity in the stands of the class and are much less frequent in the

TABLE 2 COVER-ABUNDANCE OF SELECTED SPECIES IN STANDS OF THE PRIMARY SURVEY. (Cover values less than 0.1% not indicated. See p.12 for explanation of Cover values in Table.)

[illegible]

character. Several species such as *Antennaria neglecta*, *A. racemosa*, *Aster ciliolatus* and *Senecio aureus* reach their greatest abundance and presence in the *Shepherdia* type (Table 2).

Several stands had poorly developed *Arctostaphylos* and *Shepherdia* strata, but had a well developed herb stratum dominated by *Elymus innovatus*. From the surveyed sites it was possible to distinguish two stands which were of the *Elymus* forest type (EI). More intensive work in particular areas will permit the clear description of the type, or at least clarify its relation to the *Shepherdia* and *Arctostaphylos* Types. The Cluster Analysis (Figure 6) indicates the intermediate position of the *Elymus* Type between the Moist and Xerophytic Classes.

Excluding areas of pine savanna not surveyed, there is only one type of dry pine forest - the *Arctostaphylos uva-ursi* Type (AU). It is characteristic of the warm, dry bottoms of larger and lower valleys. It is much better represented quantitatively in Jasper than in Banff. Minor phases of this type do occur. For example, *Linnaea borealis* may replace *Arctostaphylos*, or Feather Mosses may occur in small depressions and areas of greater tree cover. It is realized that these phases could be classified as forest types, thus subdividing the dry forests into smaller units based on local habitat variation, but in terms of the general survey conducted, such fine divisions were deemed impractical and unwise.

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The *Arctostaphylos* Forest Type is difficult to characterize in a positive way; the understory is very poorly developed with the exception of one or two species and these were used in the initial classification scheme. Further supporting evidence is not forthcoming from the species presence and abundance data except that the species which characterize the other forest types are absent or unimportant in this type. *Senecio cymbalarioides* has limited character value in that it is restricted to the low xeric valley bottoms of Jasper Park.

The method of cluster analysis, as described on pages 33-38, corroborated the existence of most of the nodal forest types previously recognized by using floristic and physiognomic criteria. It was also used to aid in placing stands of the primary survey into the nodal groups. Because more data were available to me concerning the stands than was included in the input to the cluster analysis, I have placed some stands in groups other than those indicated by the results of the Cluster Analysis (*viz.* stands 26-J; 32-J and 24-J; 54-J, 53-J, and 4-B; and 47-B, 39-B, 10-B, and 45-B). It can be seen by comparing Figures 5 and 6

that this regrouping has primarily affected only satellite stands and not the basic structure of the results. The regrouping emphasizes the continuous variation present in the pine vegetation of the two Parks.

The results of the cluster analysis (Figure 6) may be interpreted in terms of the three main moisture classes

of pine vegetation described at the beginning of this section. The elevational relationships of the four nodal types of the Moist Forest Class are clearly represented in Figure 6. The lower elevation *Alnus* type appears at the far left; the higher elevation *Menziesia* and *Vaccinium scoparium* types appear on the right, while the Feather Moss type with its wide elevational range extends throughout the region occupied by the moist class. Although the objectives of the primary survey did not include the determination of the frequency of the forest types, it is significant that the high elevation representatives of the Moist Forest Class came from Banff while the low elevation representatives came from Jasper.

The Mesophytic Forest Class lies between the Moist and Xerophytic Forest Classes. The two largest nodes, the *Shepherdia* and *Elymus* types, occur at mid-elevations between the generally lower, Xerophytic Forest Class and the usually higher, Moist Forest Class. The small group labelled "High Mesic" is a distinct entity throughout the cluster analysis. It represents pine stands at high elevations which do not have a characteristically well developed, moist, understory vegetation.

The Xerophytic Forest Class is closely related to the drier side of the Mesophytic Forest Class as is indicated in Figure 6 by the "bonds" linking stands in the two classes. The single nodum of the Xerophytic Class appears more closely related to the *Elymus* nodum of the Mesophytic

Class than to the *Shepherdia* nodum. This may indicate that the *Elymus* type is more xerophytic than the *Shepherdia* type.

Nearly all of the representatives of the Xerophytic Class come from Jasper. Again it was not the purpose of the Primary Survey to determine the extent and frequency of occurrence of the types of pine vegetation, but the fact that most of the Xerophytic Class is represented by Jasper sites while most of the moist class comes from Banff is indicative of a major difference between the two Parks. The main valleys in Jasper are at lower elevations, are broader and thus are warmer and drier than the major valleys in Banff. The ubiquitous pine vegetation indicates this difference between the Parks, i.e., there are proportionately more xerophytic and less moist pine forests in Jasper than in Banff.

The descriptions of the forest types which follow this section place little emphasis upon available soil nutrients. This is because variations found in available nutrients showed no correlation with recognizable forest types or variations of these types. (See section XI of available soil nutrients in intensively studied sites for information regarding seasonal fluctuations in these nutrients, p.224)

IX. DETAILED DESCRIPTION OF FOREST TYPES

A. MOIST FOREST CLASS

1: *Menziesia glabella* type-MG (e.g. 41-B, 42-B)

Forests of the *Menziesia* type occur at high elevations (i.e. over 5,500 ft. in Banff) and in other areas which also receive more moisture from precipitation or ground water or both, than do the low valley bottoms. For example about 12 cm (4.5 inches) of precipitation was measured in stand 41-B while only 9.5 cm (3.7 inches) was recorded at Banff townsite in May - August 1968 (Figure 7).

Vegetationally these forests are characterized by a nearly continuous tall shrub stratum (4-5 ft. high) dominated by *Menziesia* but including *Shepherdia canadensis* and *Rhododendron albiflorum*. The latter species is characteristic of the high subalpine forests. The dense shrub stratum has a strong influence upon the subordinate vegetation; dwarf, ericaceous shrubs like *Vaccinium scoparium*, *Phyllodoce* spp. and *Empetrum nigrum*, which presumably would otherwise be abundant in such forests, have greatly reduced populations which are mostly restricted to openings in the high shrub stratum. *Carex richardsonii*, in contrast, appears to grow quite well beneath and at the edges of the shrubs. Larger species of *Cladonia* such as *C. ecmocyna* and *C. furcata* grow in great abundance in the openings in the high shrub stratum.

As can be seen in Table 5, stands 41-B (79 years) and 42-B (69 years) are similar in age. Stands 40-B (60 years),

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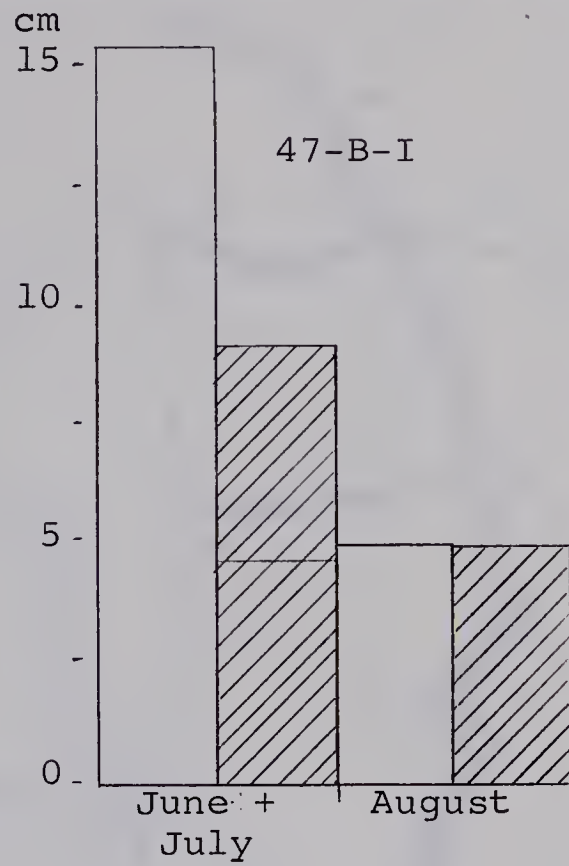
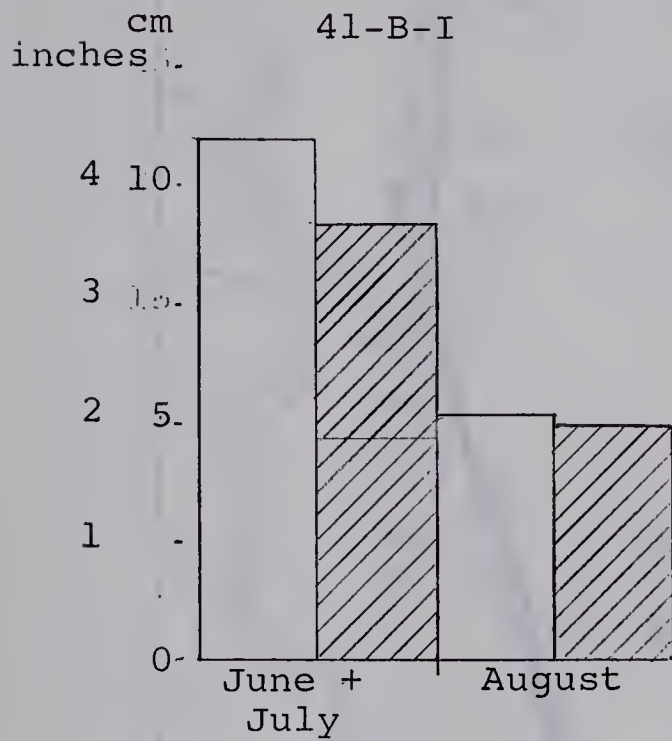
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FIGURE 7. PRECIPITATION DATA FOR INTENSIVE STANDS; 47
JUNE, JULY, AUGUST, 1968.

Banff townsite: 



Data for Banff and Jasper Townsites taken from Department of Monthly Records for June, July, and August, 1968.

Jasper townsite: 

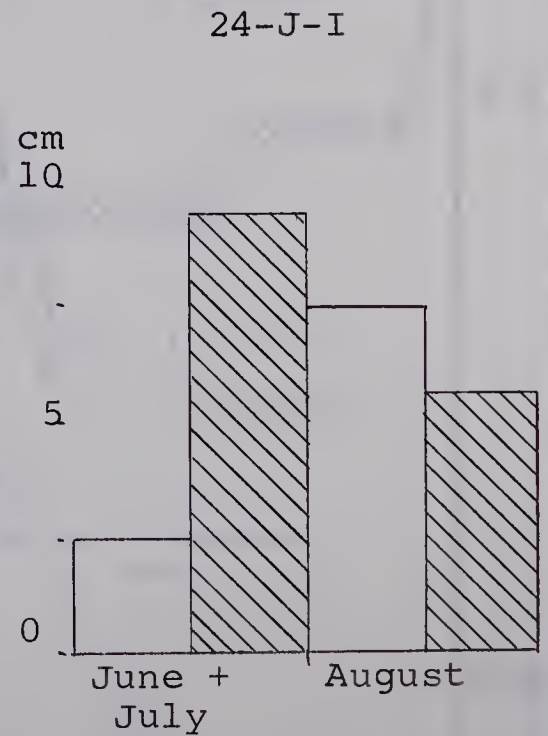
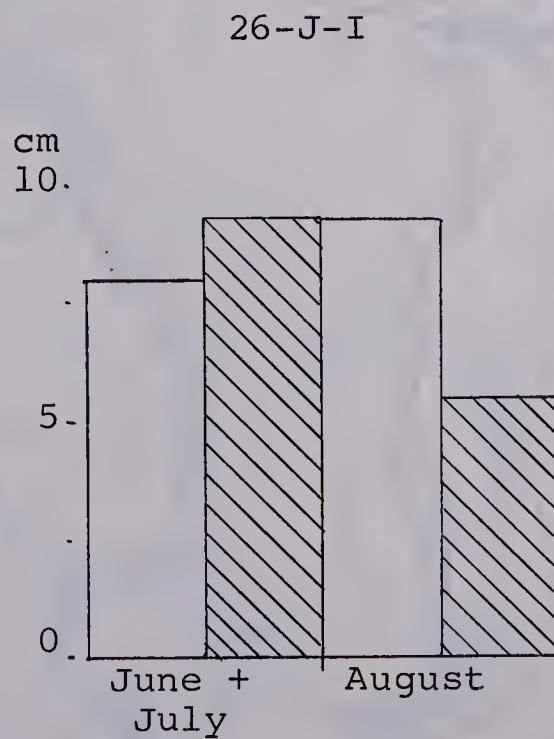
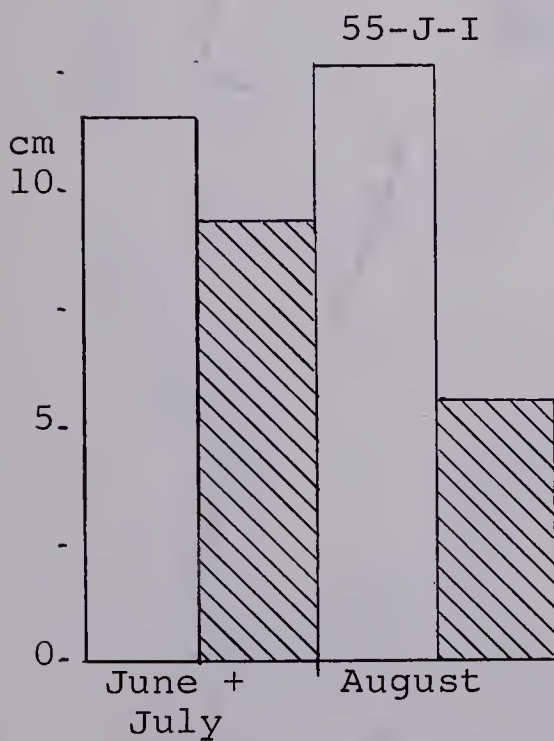


Figure 1



Figure 2



Figure 1 and Figure 2 show the results of the experiment. The y-axis represents the percentage of plants that survived. The x-axis represents the treatment groups. The hatched bars represent the control group, and the white bars represent the treated group.

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Figure 3



Figure 4



Figure 5



FIGURE 8. BANFF NATIONAL PARK SHOWING LOCATIONS OF STANDS OF THE PRIMARY SURVEY.

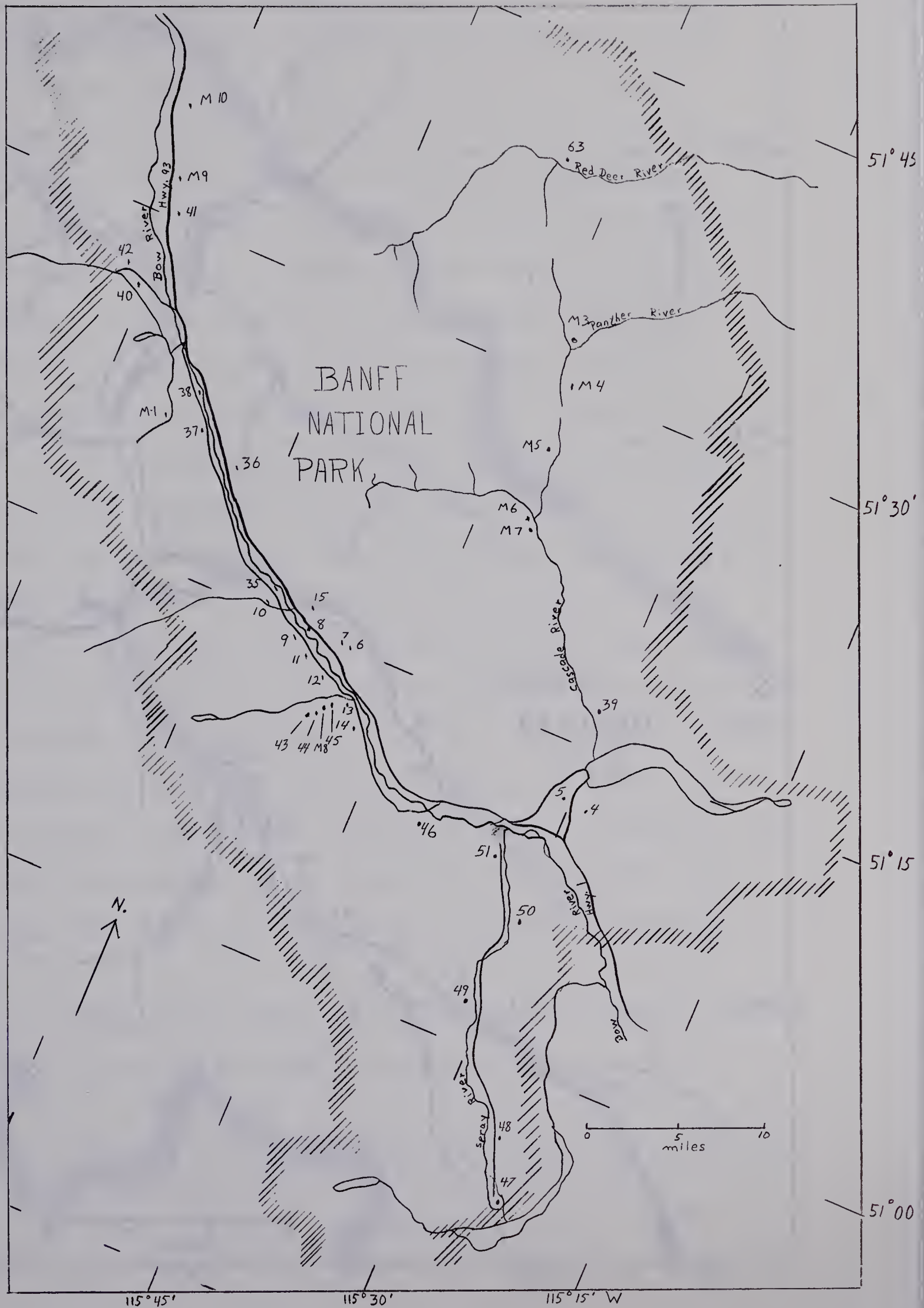
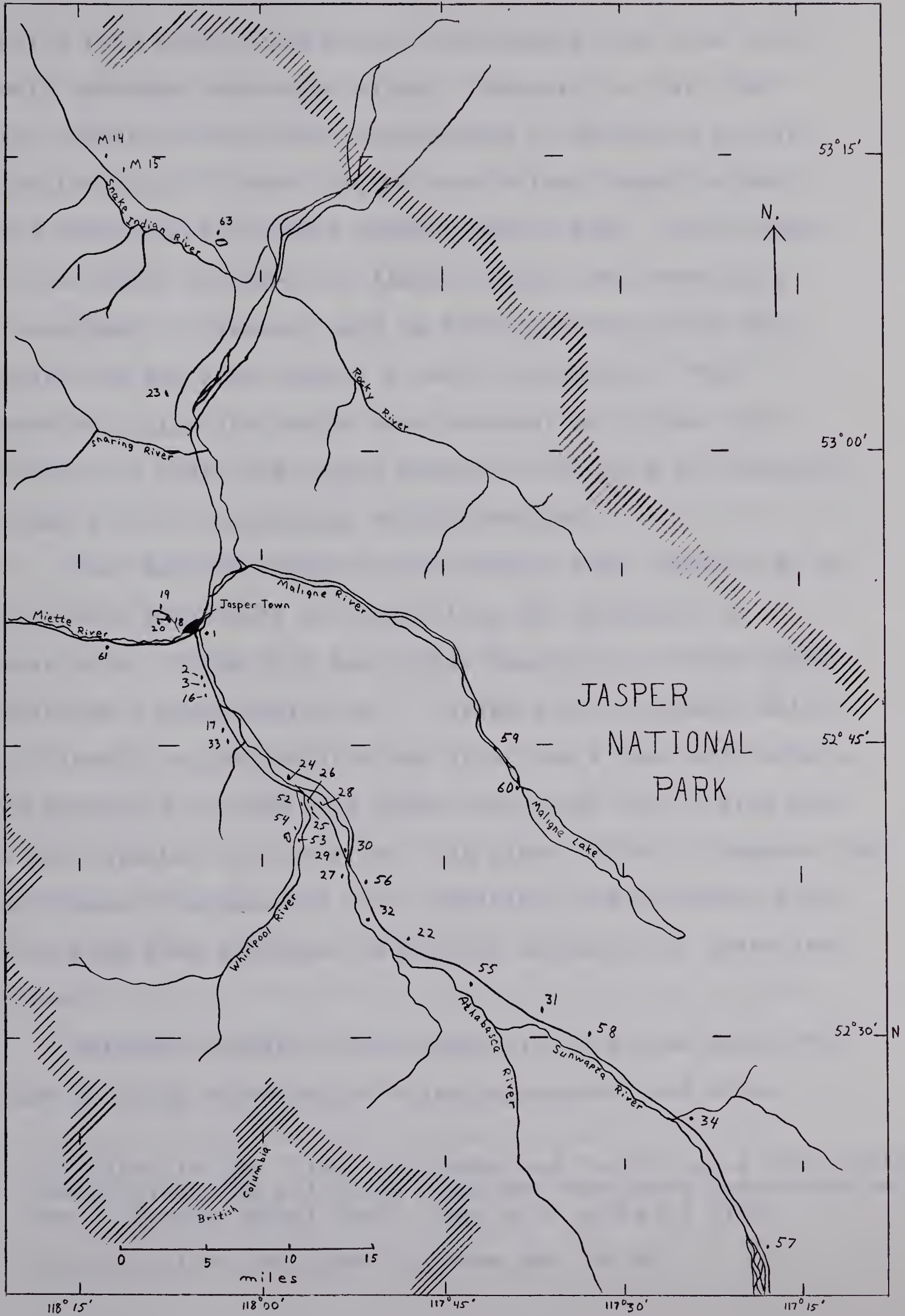


FIGURE 9. JASPER NATIONAL PARK SHOWING LOCATIONS OF STANDS OF PRIMARY SURVEY.





M-1-B (117 years), and M-10-B (125 years) also have fairly well developed *Menziesia* strata. Despite the fact that the stands with the best development of *Menziesia* are all greater than 60 years old, no conclusions regarding age and development of these forests can be made. Lutz (1956) in his study of forest of Alaska, states that *Menziesia ferruginea*¹ is present only in forests greater than 200 years old and even then as a small population. That *Menziesia glabella* can be very abundant in 80 year old forests in Banff and Jasper points to the need for intensive studies of the autecology of this species.

Tree density, when not excessively high, appears to be of little importance in controlling the abundance of *Menziesia*. Stand 41-B has a pine density of 33² and stand 42-B has a pine density of 7. Stand 43-B (61 years) which is closely related to 41-B and 42-B, has a less well developed *Menziesia* stratum than these two stands but it also has a much greater tree density - 125 pines. Thus it appears that in stands of comparable age, elevation, and available water, very high tree densities reduce the abundance of understory plants.

Surveyed forests of the *Menziesia* type show ample evidence of being succeeded by *Picea engelmannii* and *Abies*

¹ E. Hulten in the "Flora of Alaska and Neighbouring Territories (1968) gives the following synonymy: *Menziesia ferruginea* Sm. var. *glabella* (Gray) Peck, same as *M. glabella* Gray.

² Tree densities are given in stems per 100 m².

lasiocarpa. Trees of these species in all size and age classes were found in abundance while little or no pine reproduction was evident. The rapid succession to spruce and fir in these forests seems related to the more favourable habitats afforded them at higher elevations, as well as the greater availability of seed in these areas.

Identification of wood samples collected from fire-killed trees of the previous forest indicates that the present forests were preceded by spruce-fir forests with some pine. These prior forests appear to have been fairly old when burned - supporting the hypothesis that forest fires are less frequent in high, cool, moist areas than in the drier valley bottoms.

Zootic influences appeared minor in this forest type. There was a limited amount of browsing of the *Menziesia* by moose. Wood-boring ants were in part responsible for the felling of dead, standing trees. Their colonies may extend within the tree trunk from ground level to 8 ft. above ground. Eventually the bole is sufficiently weakened to break and fall during wind storms.

Because of the difficulty of access and the distance from developing population centres, these forests have not been influenced to any great extent by man. The major disruption has been from road cuts and transmission line clearings.

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2. *Alnus crispa* type-AC (stands: 25-J, 28-J, 31-J, and 33-J).

The *Alnus crispa* type is another member of the cool, Moist Forest Class which has a well-developed high shrub stratum. These forests most commonly occur at middle elevations (4000-5000 ft in Jasper and slightly higher in Banff).

Stands 25-J and 28-J are situated in the Leach Lake area, near the mouth of the Whirlpool River valley in which precipitation is high during the growing season (Figure 7) Stand 31-J is situated in the Honeymoon Lake area which also receives relatively large amounts of rain during the growing season (see Figure 7). This latter stand (31-J), although located on the southwest wall of the Sunwapta Valley, is situated on the southeast-facing slope of a small valley which runs along the side of Endless Chain Ridge. Thus on the basis of local topography the stand is situated in a cool, moist area. Stand 33-J appears to be a transitional stand of this forest type; it is not in an area of particularly high summer precipitation but there do seem to be large amounts of ground water available. Poorly defined, intermittent streams can be seen in the stand.

Vegetationally the major feature of these stands is the abundance of *Alnus crispa*, but *Vaccinium scoparium* and Feather Mosses are also important members of the community. Thus forests of the *Alnus* type show close vegetational

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affinities to cool, moist, high-elevation pine forests. They also have a high cover of *Elymus innovatus* (ca. 20-40%) which relates them to the Mesophytic Forests to be discussed later.

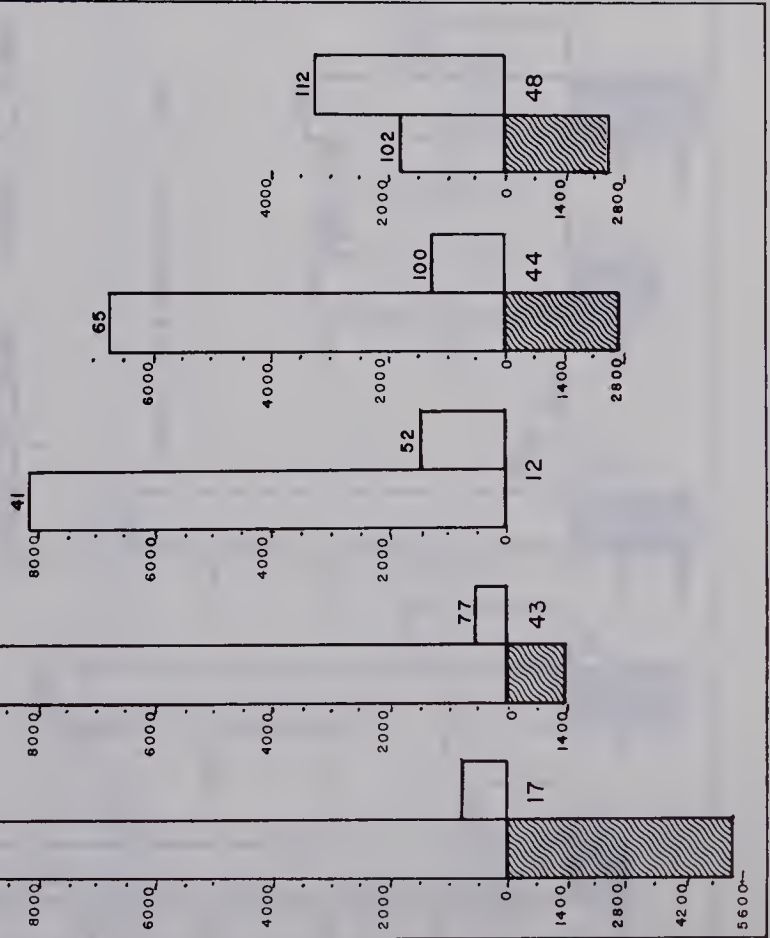
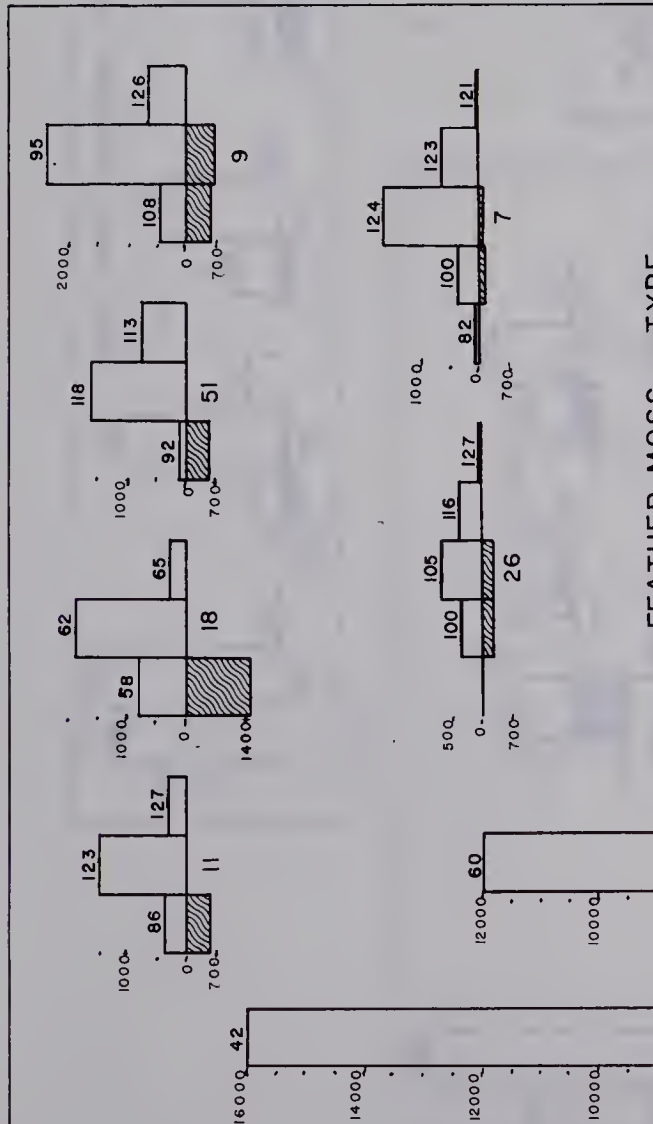
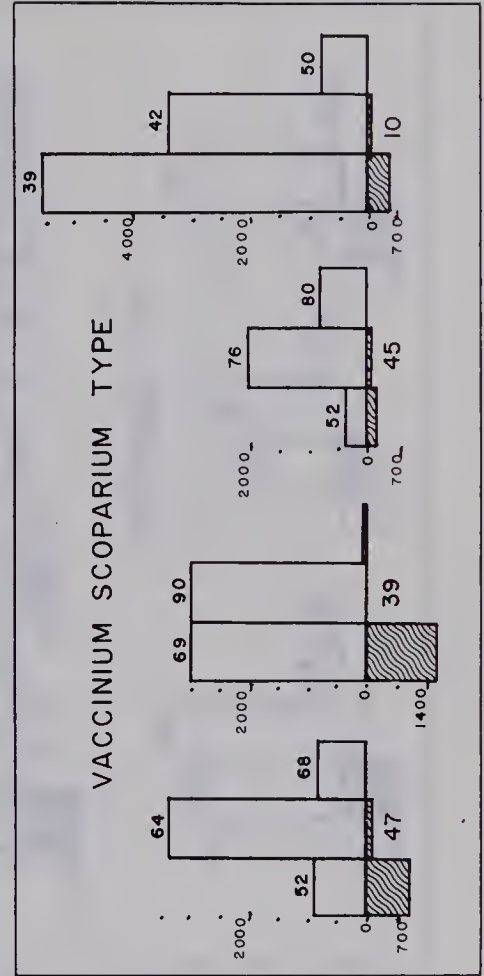
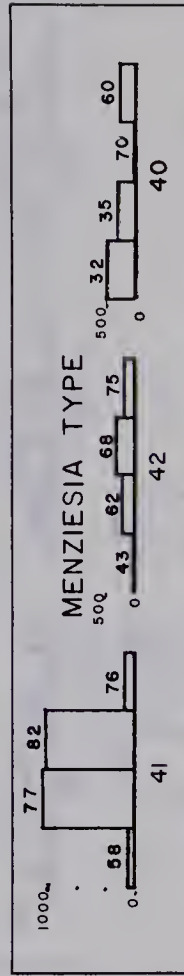
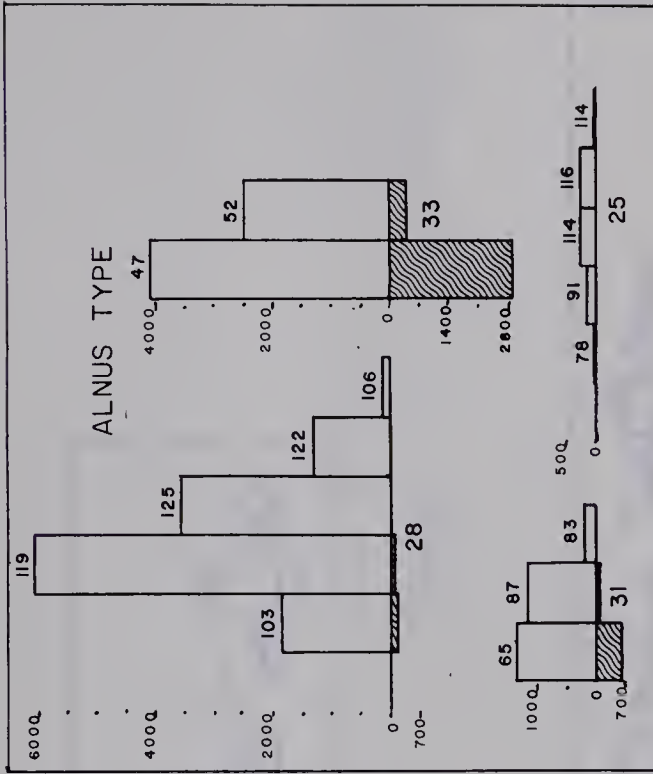
The surveyed stands range in age from 49 years (33-J) to 119 years (28-J) (Table 5). Data are insufficient to allow statements on developmental relationships except to say that this forest type is recognizable within 50 years of the time of forest establishment.

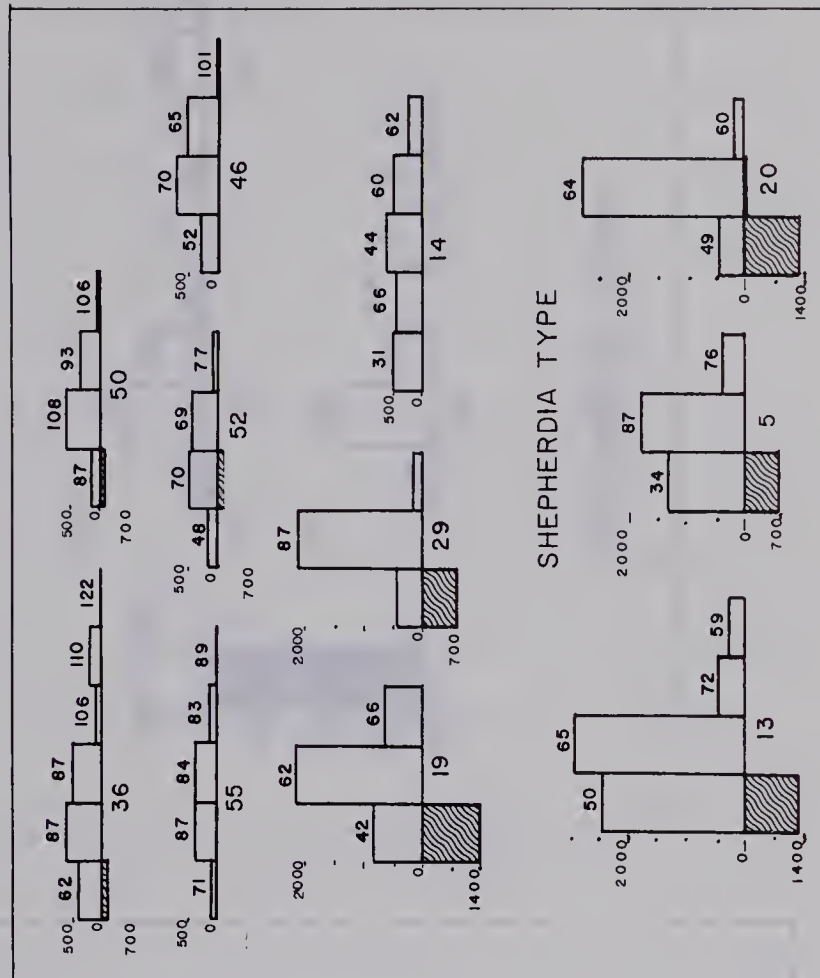
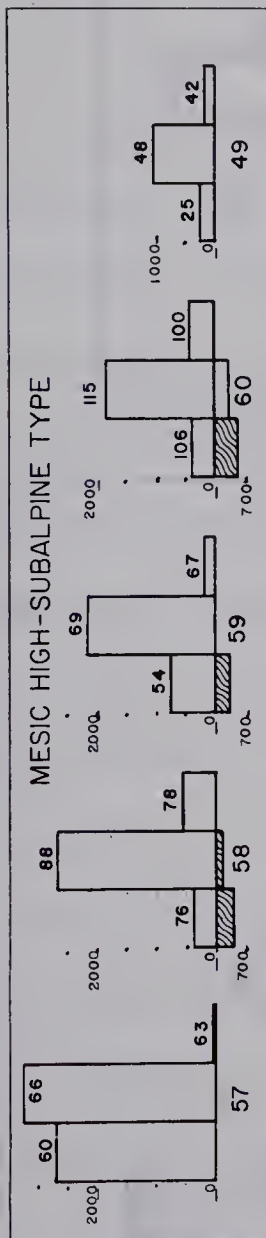
Only stand 25-J showed a moderate degree of invasion by *Picea engelmannii* and *Abies lasiocarpa*. The other stands had some reproduction of these species - more than in dry forests - but still so little as to make it obvious that succession to *Picea-Abies* forests is very slow.

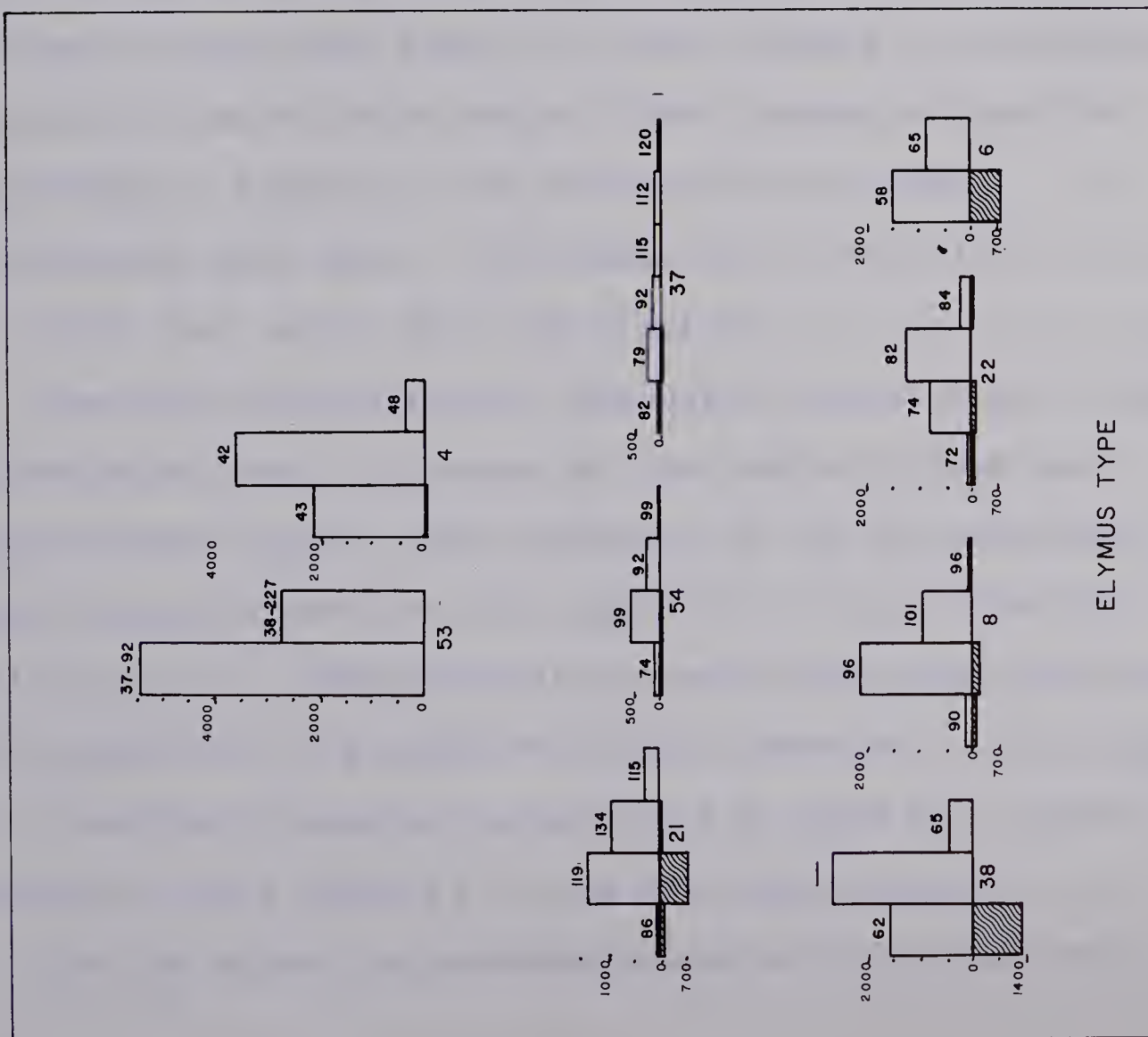
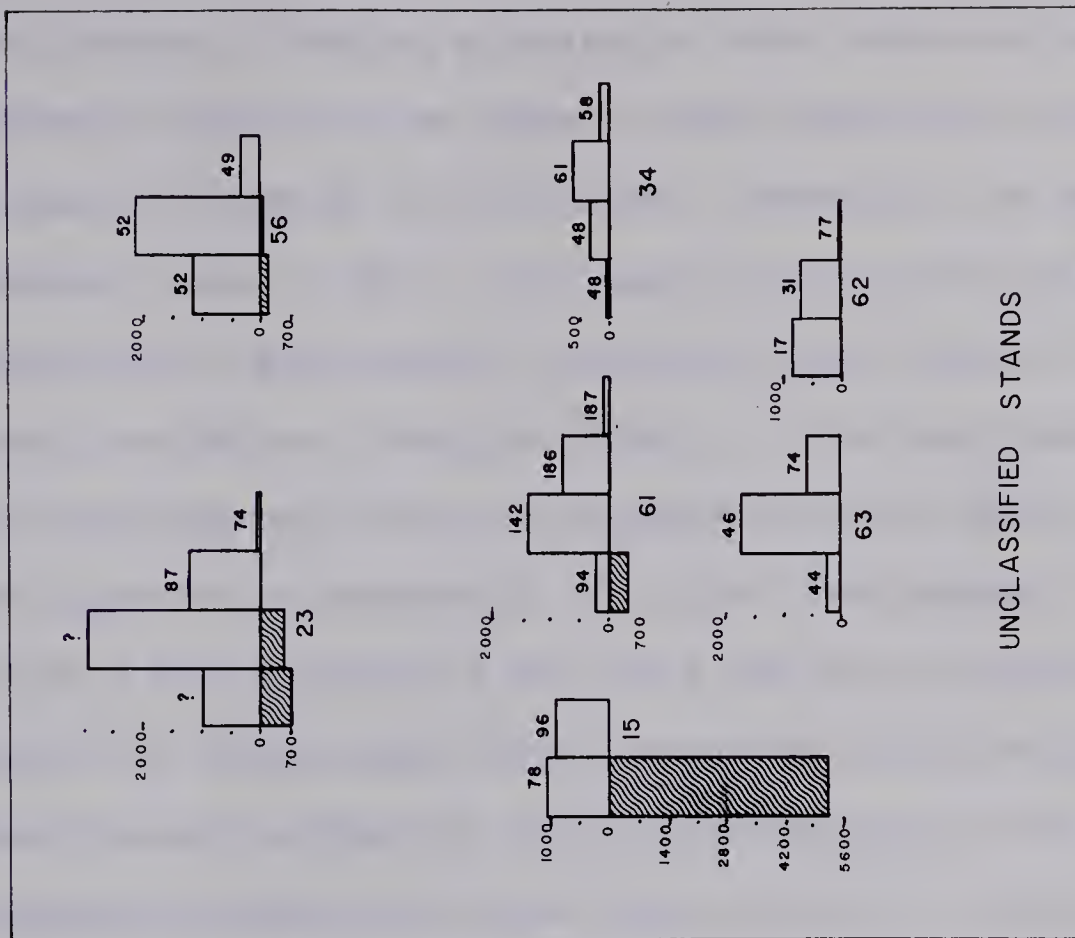
Vascular species diversity ranges from a low of 34 in 25-J to a high of 51 in 28-J. Large portions of the ground in 25-J are covered only with needle litter or a very sparse moss carpet, whereas a luxuriant, continuous carpet of vegetation covers the forest floor in 28-J. The latter stand supports large populations of *Elymus innovatus*, *Linnaea borealis*, *Cornus canadensis*, and *Aster ciliolatus*, to mention a few. The 18 cm rooting horizon in 25-J is a loamy sand with 10% available water in the less than 2 mm fraction of the soil. The 13 cm rooting zone in 28-J is a sandy loam and has 24% available water. It is possible that the greater species diversity in 28-J is attributable to more available water since these two stands, being only

FIGURE 10. HISTOGRAMS OF TREE-DIAMETER DISTRIBUTIONS

Each bar of the histogram represents a 3-inch tree diameter size class, *i.e.* 1-3, 3-6, 6-9, etc. Each histogram begins with the 1-3 inch class. The height of the bars is proportional to density (No. of stems per hectare). The shaded bars represent standing, dead trees and the unshaded bars represent living trees. The number below each histogram is the stand number, while the numbers above each bar represent the approximate ages of individuals of the class.







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above two stands. Seeding appears to have occurred over a much greater length of time than in the former two stands. The age span is from 85 to 125 years. Mortality is greater in the denser stand - 28-J. Increment cores show sustained and exceptionally good growth throughout the life of the trees (the best of any stand studied). It is not known why tree densities are low and regeneration was slow in an area that appears so favourable for pine development. Basal areas of 29.5 for stand 25-J and 32.4 for 28-J support the hypothesis that these areas are favourable for pine growth.

These forests appear to be only occasionally used by large ungulates such as elk, but many of the few *Abies* present in the stand have been severely browsed. For the most part though, the effect of large animals is negligible. Man also has made little use of these forests except for some areas of logging in the Whirlpool River area.

3. Feather Moss type - FM (stands 26-J, 18-J, 17-J, 7-B, 12-B, 9-B, 44-B, 43-B, 48-B, 51-B)

The third subdivision of the Moist Forest class is the Feather Moss type. It occurs in the middle to high sub-alpine forest region. The altitudes of the low elevation feather moss forests are 26-J (3,800 ft), 18-J (4,000 ft), 17-J (4,100 ft). Mid-elevation forests are exemplified by 51-B (4,700 ft.), 7-B (4,800 ft.), 11-B (4,900 ft.), 12-B (5,000 ft.), and high elevation forests by 9-B (5,400 ft.), 44-B (5,600 ft), 43-B (5,700 ft.), and 48-B (6,000 ft).

The low elevation representatives of this type are

valley bottom stands from Jasper, while the first two mid-elevation representatives are from valley bottoms in Banff. The difference in mean altitude between these two groups is about 1,000 ft. This figure may represent the compensation in elevation to be expected with the increase in latitude from Banff to Jasper. The 1,000 ft compensation is the same as that determined from the *Shepherdia* forest-type data (see p. 76). This compensation figure for the Feather Moss Forest type should be viewed with caution because of the small number of samples used in its calculation (see however, substantial agreement in Stringer p.213, 1966).

Stand 26-J, although quite low in elevation, is located very close to 25-J and 28-J and thus also receives much summer precipitation (Figure 7). Its site on the first and second terraces of the Whirlpool River presumably indicates a high water table; thus it is reasonable to describe the stand as part of a cool, moist forest.

Stand 18-J is located just south of Cabin Lake Reservoir in an area of numerous lakes, and receives more than average rain from storms which come down the Miette River Valley. Stand 17-J is located near 33-J and thus can be described as a cool, moist forest for similar reasons (p. 52). Stand 51-B, besides receiving water from fairly heavy precipitation, receives surface ground water draining from the upper slopes of Sulphur Mtn. This stand, having a north-east aspect, is kept cool because of its low solar radiation load even in late June and July. Stand 7-B is situated in the vicinity of

much storm activity associated with the Storm Mtn.-Mt. Eisenhower area. It is also located on a low valley bench which intercepts ground water draining from higher slopes. Stands 9-B, 11-B, and 12-B, are located on the lower, steep, northeast slopes of Copper Mtn. They are kept as cool, moist forests by their aspect, slope position, and geographic location in the same storm area as stand 7-B. Stands 44-B and 43-B are located on northwest slopes of Pilot Mtn. in the Redearth Creek Valley - a valley which also appears to receive above average summer rain. Thus these stands may be thought of as cool and moist for reasons similar to those used for stands 9-B, 11-B, and 12-B. Finally, stand 48-B belongs in the Moist Forest Class because of its elevation, location on a steep mountain slope, and because it is situated in the narrow Spray River Valley which receives large amounts of precipitation.

This forest type is a variable one as might be expected considering the simple criterion upon which it is based: the presence of large populations of feather mosses. As will be discussed later, many of these forests might better be described as variants of the other cool, moist forest types. Nevertheless, stands such as 9-B, 11-B, 12-B, and 48-B do represent a modal type for the feather moss forest.

The typical *Pinus contorta* feather moss forest is characterized by a continuous or nearly continuous moss carpet. In the places studied, it averages about 15 cm thick and is composed primarily of *Hylocomium splendens* and *Pleurozium*

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schreberi. Other mosses may be locally abundant as microhabitats permit, as for example *Dicranum polysetum* on rotting wood, but this is not characteristic of the forest as a whole. The modal feather moss forest has very little vascular understory vegetation, in strong contrast to the other forest types. But as mentioned previously, sparsity of subordinate vascular vegetation does not necessarily imply low species diversity. Vascular species diversity is variable, from a low of 29 in 48-B to a high of 49 in 9-B, but evidently is not related to Available Water in the rooting zone as was the case in forests of the *Alnus* type.

The minimum time required for a feather moss carpet to develop in a forest is not known, but from stand-age data it would appear that such development is complete within 40 years following forest establishment.

Within the range of tree densities covered in the stands of this forest type, tree density does not seem to be a significant controlling factor relative to the feather mosses. Densities range from 22 in 11-B to 125 in 43-B. To what extent the density of overstory vegetation may affect the establishment and productivity of the feather mosses is not known.

Data gathered concerning substrate are inadequate to permit correlation with variability in this forest type. It may be significant though, that the modal feather moss forests all occur on very shallow soils overlying bedrock. Weetman & Timmer (1967) hypothesized that the moss carpet may serve

as a major source of nitrogen for *Picea mariana* growing over bedrock in eastern Canada. Although the results of tests for available nutrients in the humus of these pine forests showed no significant peak in forests with feather moss carpets, this does not disprove the hypothesis, for detailed analyses with this objective in mind were not carried out. Further, it is possible that the level of nitrogen which was measured may be due to the presence of the mosses, i.e. without them there may be considerably less nitrogen available. Thus a symbiotic nutrient as well as moisture relationship may exist between the feather mosses and trees.

Diameter distributions (Figure 10) of the trees are of the two forms (young and mature) described above for the *Alnus* forest type. This may indicate that the feather moss type becomes well differentiated at an early age (e.g. 43 years in 12-B) and maintains its characteristic structure during the development and maturation of the pine forest as exemplified by stands 9-B and 11-B. These two with stand 48-B are the oldest stands of this type studied and show signs of being succeeded by *Picea* and *Abies*. The majority of the *Picea* and *Abies* trees present follow a similar diameter size-class distribution to the pine, indicating that these spruce and fir probably became established about the same time as the pine. The maximum ages of *Picea* (119 years 9-B, 110 years 11-B, 116 years 48-B) in these stands support this hypothesis. These trees probably are seed sources for the abundant regeneration of these species.

As stated earlier, there are many stands classed in the feather moss type which might be classed with other cool, moist forest types, or even the moister members of the mesic forests. Stands 43-B, and 44-B, in addition to having a well-developed feather moss carpet, have a discontinuous cover of *Menziesia glabella*. They occur at a similar elevation and are similar in age to the two *Menziesia* forests 41-B and 42-B, but the former two have a much denser tree stratum and a very different tree population structure from the *Menziesia* stands. Stands 43-B and 44-B are very close to what are called "stagnant" pine forests. Height and diameter growth are far behind that of 41-B despite the similarity in basal area of pine which Smithers (1961) describes as being one of the best indicators of site potential. It may be then, that the high tree density not only retards normal tree maturation, but also retards community development. Thus stands 43-B and 44-B might eventually develop into the *Menziesia* forest type if tree density declines sufficiently.

Stand 18-J has distinct affinities with the *Alnus* forests, the *Shepherdia* forests, and the *Elymus* forests. It is heterogeneous both floristically and physiognomically. There are large areas without significant shrub cover in which *Elymus* and other herbs are quite abundant and are underlain by moss carpet. These open areas are separated by areas where either *Shepherdia* or *Alnus* is abundant. This stand represents a mosaic of forest types.

The index of similarity used in the numerical analysis

of the data, being based solely upon cover estimates, is controlled by species which have large cover values. Thus 18-J is most closely associated with the feather moss group because of the high cover of feather mosses. Although the numerical analysis does not indicate the relationship, the presence of a moderately large population of *Shepherdia* does indicate an affinity with that group.

A stand such as 18-J clearly indicates that the factors controlling the differentiation of the major forest types being described here are not mutually exclusive, but overlap to a large extent.

4. *Vaccinium scoparium* type-VS (Stands 10-B, 39-B, 45-B, 47-B)

The *Vaccinium scoparium* type is not as well represented in stands of the Primary Survey as are some of the other forest types. It consists of two phases - a high elevation, moist phase and a low elevation, mesophytic phase. The type seems to be most abundant on an areal basis in the high subalpine forests above the *Menziesia* zone. Unfortunately none of these sites were included in the Primary Survey. Stand 47-B is a close approximation of this phase while stands 10-B and 45-B are good representatives of the less extensive lower elevation phase.

Stand 47-B is located at an elevation of 5,800 ft. on a small flat plateau above the south end of the Spray River in Banff. It receives summer precipitation in excess of 20 cm (Figure 7). Vegetationally the stand is characterized by the abundance of *Vaccinium scoparium* plus locally

abundant patches of *Cladonia ecmocyna*, *C. cenotea*, *C. furcata*, and *C. multiformis*. *Menziesia glabella* and *Shepherdia canadensis* form a very thin, discontinuous high shrub stratum. The very good development of *Arnica cordifolia*, *Aster ciliolatus*, and *Lycopodium annotinum* found in this stand typifies many of the cool moist forest types.

Stand 39-B is similar to 47-B in that it has a moderately well developed dwarf-shrub stratum of *Vaccinium scoparium* underlain by a feather moss carpet. It differs in that it has a discontinuous high shrub stratum which is co-dominated by *Shepherdia*, *Ledum groenlandicum*, and *Ledum glandulosum*. The presence of a moderately large population of *Vaccinium vitis-idaea* also makes it somewhat different from the more typical forests of this type.

Because of the lack of representative stands of this phase, nothing can be said about the correlation of stand age with development of this type. For a discussion of the effect of tree density upon the understory flora, see the discussion of the intensive stand 47-B-I (p.134).

The mesophytic *Vaccinium scoparium* phase is exemplified by stands 45-B and 10-B. They are situated on benches formed from rocky, lateral moraines. The understory of both sites is dominated by a continuous or nearly continuous dwarf shrub stratum of *Vaccinium scoparium* with *Vaccinium caespitosum* interspersed throughout. Feather mosses are present in both stands but are not structurally important in either.

Stand 10-B may not remain in the *Vaccinium scoparium* forest type. The stand is young (40 years) and is situated in an area of heavy precipitation associated with the Storm Mtn. region. The stand is in the centre of an extensive burn. Tree density is fairly high (90). Sparse population of *Menziesia* and *Cladonia* spp. are present but herb diversity is average (37 species). The elevation of the stand is 5,200 ft. It is possible that, as this stand matures, tree density decreases, and sufficient time elapses during which more plant species may invade the area, it will develop into the *Menziesia* type of pine forest.

On the north stand 10-B grades into a low wet area of *Picea glauca/engelmannii* with a dense understory of *Alnus*. This may be indicative of the different habitats in which *Vaccinium scoparium* and *Alnus crispa* grow best - the *Alnus* in areas where ground water is more consistently in greater supply as would occur where the water table is higher, and the *Vaccinium* in areas of high precipitation but without high soil moisture. A comparative study of actual soil moisture throughout the growing season in these two areas would add greatly to our knowledge of the optimal habitats of these two species in this area.

Although *Vaccinium scoparium* is predominately a high subalpine species it does occur at lower elevations (4,800 ft) in the valley bottoms and lowest slopes where the environment is warmer and drier. It may be a subordinate species of stands such as 14-B and 37-B or it may be a major species

as in 45-B.

The mature mesophytic *Vaccinium* forest phase, as exemplified by 45-B, is closely related to the moist *Shepherdia* forest type, e.g. 14-B and 36-B. In this phase the *Vaccinium* occurs as large aggregations of healthy, vigorous plants and *Shepherdia* occurs as a small population of widely-spaced plants. Lichens such as *Cetraria ericetorum*, *Cladonia furcata*, and *Peltigera canina* are very abundant except where tree densities are greater and here small patches of feather mosses and *Peltigera aphthosa* occur.

A wet slough-like area occurs at the east end of stand 45-B. The pine continues essentially uninterrupted out to the edge of the water but understory vegetation changes dramatically. The presence of 3 - 4 ft high transgressives of *Populus balsamifera* within the stand proper, indicates that soil moisture must be readily available for long periods of time. The fact that the largest *P. balsamifera* were dead individuals about 5 ft high may indicate that this species is particularly susceptible to browsing by elk and deer which use these forests as part of their range.

As with most of the valley bottom forests, succession to other tree species appears to be very slow. A few *Picea* and *Abies* trees were present but new reproduction was nil.

B. MESOPHYTIC FOREST CLASS

5. Mesophytic High Subalpine Forests (stands 57-J, 58-J, 59-J, 60-J, and 49-B)

The cluster analysis separated these stands as a distinct unit (Figure 5 and 6) but associates them with the high subalpine Feather Moss forest-type. These are all high elevation stands (5,400 - 6,100 ft) that do not have well developed *Menziesia*, *Vaccinium scoparium*, or feather moss strata; these species are present but their population sizes are small. *Ledum groenlandicum* and *Vaccinium vitis-idaea* are more abundant here than in most of the other high elevation stands.

Relatively little is known about precipitation received by these stands, as they occur in areas which I visited much less frequently and meteorological data are not kept regularly. Stands 57-J and 58-J, being at high elevations on southwest-facing valley walls of Sunwapta Pk. and Endless Chain Ridge respectively, would be expected to receive relatively large amounts of precipitation and solar radiation. No precipitation data are available from the upper Maligne River stands - 59-J and 60-J.

Concomitant with the high elevation of these stands is a shortening of the growing season. For example, in stand 60-J which was sampled August 25, 1966, *Linnaea borealis* was in bud and in flower, *Cornus canadensis* was flowering, and *Vaccinium vitis-idaea* had small, green fruits. Stand 59-J was only slightly more advanced. At lower elevations the *Linnaea* and *Cornus* had ripening fruits and the *Vaccinium* had ripe, red fruits. Thus some of these high subalpine forests experience a very much shortened growing season, at

least during some years. This is probably a significant factor in causing the very low vascular species diversity of these two stands. 25 vascular species were recorded in 59-J and 27 in 60-J.

The four Jasper stands have fairly even-aged pine populations indicating fairly rapid pine regeneration following fire (see Figure 10). Each stand had charcoal in the humus and the remains of dead, burnt trees, indicating the occurrence of fire in the past. Stand 49-B is only half as dense (15) as the Jasper stands (Figure 10) and has a wide range of ages indicating that pine regeneration has been slow and in fact is still in progress in the numerous large openings.

Stands 58-J and 60-J are good examples of maturing pine forests of moderate density. The majority of the living trees are not in the smallest nor the largest diameter size classes (Figure 10). Thinning is progressing and the greatest mortality is in the smallest diameter class. Stands 49-B and 59-J are similar to these two stands but mortality is much lower. Stand 57-J shows signs of stagnation in that its density is twice that of the other stands of this group (60) and nearly all of the trees fall in the two smallest size classes with similar numbers in each class. Mortality is negligible. The stagnating effect appears to be only affecting diameter growth and tree mortality. The four Jasper stands have similar tree heights and crown depths despite the density differences (Table 3).

TABLE 3. TREE HEIGHT AND CROWN DEPTH OF PRIMARY SURVEY STANDS

| | | Tree Height (m) | | | | Crown Depth (m) | | | |
|-----|--------------|-----------------|----------|------|------|-----------------|----------|------|------|
| | | Mean | St. dev. | Max. | Min. | Mean | St. dev. | Max. | Min. |
| MG | 41 | 17.9 | 5.88 | 25.1 | 8.7 | 8.6 | 5.02 | 15.1 | 1.4 |
| | 42 | 12.8 | 4.41 | 19.2 | 5.9 | 10.1 | 3.97 | 14.6 | 3.2 |
| | 40 | 13.8 | 3.87 | 17.8 | 7.8 | 10.4 | 3.07 | 15.1 | 6.4 |
| | Group totals | 14.8 | 2.70 | | | 9.7 | 0.96 | | |
| AC | 25 | 27.1 | 6.01 | 32.4 | 12.8 | 16.2 | 5.58 | 22.9 | 6.4 |
| | 28 | 24.2 | 4.25 | 28.3 | 14.6 | 12.2 | 3.30 | 16.5 | 6.4 |
| | 31 | 18.4 | 6.87 | 26.5 | 8.7 | 7.9 | 5.28 | 14.6 | 2.3 |
| | 33 | 14.8 | 3.51 | 19.2 | 9.6 | 8.6 | 2.90 | 12.3 | 4.6 |
| | Group totals | 21.1 | 5.56 | | | 11.2 | 3.81 | | |
| FM | 26 | 25.5 | 6.52 | 31.5 | 13.7 | 13.5 | 5.65 | 20.1 | 4.6 |
| | 18 | 16.7 | 3.55 | 20.6 | 12.3 | 7.4 | 3.09 | 11.4 | 4.6 |
| | 17 | 10.0 | 2.89 | 14.6 | 6.4 | 4.4 | 1.79 | 7.3 | 2.7 |
| | 7 | 23.9 | 3.97 | 27.4 | 17.4 | 16.0 | 3.35 | 19.2 | 11.0 |
| | 11 | 17.9 | 2.07 | 20.1 | 14.6 | 7.4 | 2.51 | 6.4 | 4.1 |
| | 12 | 13.2 | 4.47 | 19.2 | 7.8 | 8.0 | 3.45 | 12.3 | 3.2 |
| | 9 | 16.2 | 5.62 | 22.4 | 7.3 | 6.8 | 4.07 | 11.9 | 2.7 |
| | 44 | 11.0 | 1.92 | 13.3 | 8.2 | 3.7 | 1.53 | 5.5 | 1.8 |
| | 43 | 7.8 | 1.65 | 9.1 | 5.9 | 3.9 | 1.47 | 5.0 | 2.3 |
| | 48 | 14.0 | 2.90 | 18.3 | 10.5 | 4.0 | 1.22 | 5.0 | 2.3 |
| | 51 | 19.2 | 5.74 | 26.5 | 11.4 | 8.4 | 3.46 | 14.2 | 4.6 |
| | Group totals | 15.9 | 5.54 | | | 7.6 | 3.99 | | |
| VS | 47 | 14.9 | 3.19 | 18.7 | 11.0 | 6.9 | 3.10 | 11.4 | 2.7 |
| | 39 | 12.2 | 4.38 | 16.9 | 6.9 | 5.7 | 2.13 | 7.8 | 2.7 |
| | 10 | 11.7 | 3.28 | 14.6 | 7.3 | 5.6 | 3.24 | 9.6 | 2.7 |
| | 45 | 16.4 | 3.67 | 20.6 | 11.9 | 8.0 | 3.11 | 11.4 | 4.6 |
| | Group totals | 13.8 | 2.23 | | | 6.6 | 1.13 | | |
| MHS | 49 | 14.5 | 3.90 | 16.9 | 8.7 | 11.7 | 3.47 | 15.1 | 6.9 |
| | 57 | 15.9 | 4.82 | 23.8 | 11.4 | 7.4 | 2.54 | 9.6 | 2.7 |
| | 58 | 17.6 | 4.60 | 20.6 | 9.6 | 6.4 | 2.33 | 8.7 | 3.7 |
| | 59 | 13.5 | 3.51 | 15.5 | 8.2 | 6.2 | 2.06 | 7.8 | 3.2 |
| | 60 | 16.6 | 3.14 | 20.1 | 11.4 | 6.3 | 1.43 | 8.2 | 4.1 |
| | Group totals | 15.6 | 1.64 | | | 7.6 | 2.34 | | |
| SC | 46 | 18.6 | 5.77 | 27.8 | 8.2 | 11.4 | 4.63 | 19.2 | 5.0 |
| | 36 | 20.5 | 6.12 | 25.1 | 6.9 | 11.5 | 3.46 | 14.6 | 4.1 |
| | 14 | 16.4 | 5.16 | 23.8 | 6.9 | 11.2 | 5.44 | 17.8 | 4.1 |
| | 50 | 16.8 | 5.05 | 22.4 | 8.2 | 12.4 | 6.29 | 20.1 | 2.7 |
| | 13 | 15.9 | 4.18 | 21.0 | 8.2 | 10.8 | 4.95 | 17.8 | 3.2 |
| | 20 | 15.2 | 3.94 | 20.6 | 9.1 | 9.1 | 5.43 | 18.3 | 2.7 |
| | 55 | 20.9 | 6.93 | 27.0 | 6.4 | 12.8 | 6.44 | 20.6 | 2.3 |
| | 52 | 16.4 | 5.13 | 22.9 | 7.3 | 11.3 | 4.41 | 15.5 | 3.7 |
| | 19 | 18.2 | 5.02 | 22.9 | 11.0 | 12.5 | 6.05 | 19.7 | 3.2 |
| | 29 | 19.2 | 5.82 | 25.6 | 9.1 | 10.2 | 4.73 | 15.1 | 4.1 |
| | 5 | 15.5 | 2.29 | 17.8 | 12.3 | 11.2 | 4.55 | 15.5 | 4.6 |
| | Group totals | 17.4 | 1.92 | | | 11.3 | 1.06 | | |

Table 3 cont'd.

| | | Tree Height | | | | Crown Depth | | | |
|--------------|----|-------------|----------|------|------|-------------|----------|------|------|
| | | Mean | St. dev. | Max. | Min. | Mean | St. dev. | Max. | Min. |
| AU | 1 | 15.9 | 2.90 | 18.3 | 10.1 | 11.9 | 4.38 | 16.5 | 3.7 |
| | 2 | 17.6 | 3.01 | 19.7 | 11.0 | 12.7 | 3.45 | 16.9 | 7.3 |
| | 3 | 12.2 | 2.85 | 16.0 | 9.1 | 5.9 | 1.98 | 8.7 | 4.1 |
| | 16 | 11.2 | 3.24 | 15.1 | 6.4 | 6.1 | 2.77 | 11.0 | 3.2 |
| | 24 | 17.0 | 5.73 | 22.4 | 6.4 | 7.6 | 4.64 | 13.7 | 2.7 |
| | 27 | 15.1 | 4.76 | 21.5 | 7.8 | 9.0 | 4.47 | 15.1 | 5.5 |
| | 30 | 12.1 | 4.37 | 16.9 | 7.3 | 8.6 | 4.83 | 13.7 | 3.2 |
| | 32 | 15.8 | 5.75 | 24.7 | 7.8 | 9.1 | 4.33 | 14.6 | 4.1 |
| | 35 | 10.0 | 1.76 | 11.9 | 8.2 | 4.1 | 1.34 | 5.5 | 2.3 |
| Group totals | | 14.1 | 2.75 | | | 8.3 | 2.79 | | |
| EI | 38 | 15.4 | 5.47 | 25.1 | 5.9 | 10.7 | 5.21 | 20.1 | 3.7 |
| | 37 | 18.8 | 6.22 | 25.1 | 6.9 | 14.4 | 5.53 | 20.6 | 3.7 |
| | 21 | 20.0 | 6.60 | 27.4 | 7.8 | 11.6 | 6.86 | 21.5 | 1.8 |
| | 54 | 22.2 | 6.52 | 33.8 | 13.7 | 12.4 | 3.74 | 18.3 | 6.4 |
| | 53 | 12.7 | 3.11 | 16.5 | 8.2 | 7.7 | 2.22 | 10.1 | 4.1 |
| | 4 | 15.4 | 2.80 | 18.3 | 10.1 | 10.1 | 3.28 | 14.6 | 6.4 |
| | 8 | 20.9 | 4.00 | 23.8 | 12.8 | 14.5 | 5.00 | 20.1 | 9.1 |
| | 22 | 19.0 | 5.68 | 21.5 | 8.7 | 10.1 | 4.20 | 6.0 | 4.6 |
| | 6 | 15.4 | 4.67 | 21.9 | 14.2 | 4.8 | 1.15 | 5.9 | 3.7 |
| Group totals | | 17.8 | 3.15 | | | 11.2 | 3.09 | | |
| RES | 23 | 14.3 | 2.54 | 17.4 | 11.4 | 7.3 | 2.56 | 11.0 | 5.0 |
| | 61 | 13.7 | 2.36 | 16.5 | 10.1 | 8.0 | 2.65 | 12.3 | 4.1 |
| | 34 | 12.5 | 4.30 | 17.4 | 6.9 | 10.3 | 4.09 | 15.1 | 5.5 |
| | 56 | 12.9 | 2.60 | 16.5 | 10.1 | 8.6 | 2.52 | 12.8 | 5.5 |
| | 63 | 16.1 | 4.10 | 11.4 | 20.6 | 5.4 | 2.62 | 2.3 | 7.8 |
| | 62 | 12.5 | 4.86 | 16.9 | 5.5 | 9.4 | 4.41 | 14.6 | 4.6 |
| | 15 | 11.4 | 3.56 | 16.0 | 7.8 | 4.1 | 1.78 | 6.4 | 1.8 |
| Group totals | | 13.3 | 1.53 | | | 7.6 | 2.19 | | |

The four sites have similar basal areas (Table 4) which would tend to indicate that the sites were comparable in their potential forest production.

Three of the four Jasper stands have a thick surface horizon (approx. 20 cm) with a relatively high Available Water potential. 58-J though, is unique amongst the five stands of this type in that the surface 50 cm is underlain by a clay horizon 12 cm thick. Although the water-holding capacity of this horizon is low and similar to the surface one (approx. 8% available water), the high clay content of the lower and very compact horizon may make it less permeable to water and thus tend to concentrate water in the surface soil. Water from direct precipitation higher up on Endless Chain Ridge would tend to flow on top of this horizon if it were extensive enough laterally. Such a mechanism could provide a supply of water sufficient to compensate for the lower water holding capacity of the soil.

A further indication of the general wetness of 58-J which lends support to the "perched water table" hypothesis is the presence of typically moist habitat species such as *Carex vaginata*, *Streptopus amplexifolius*, and *Parnassia* sp. in addition to a developing understory of *Picea mariana*. The herbaceous wetland species are not so abundant as to play a significant role in the cluster analysis and thus stand 58-J is not isolated from the mesic high subalpine group despite its slightly different species composition.

Stand 49-B was the driest of the mesic, high subalpine

Table 4 concluded

| | Mean | St. Dev. | Mean | St. Dev. | Mean | St. Dev. | Mean | St. Dev. | Mean | St. Dev. | Mean | St. Dev. |
|--------------|------|----------|------|----------|------|----------|------|----------|------|----------|------|----------|
| 8 | 25.3 | 10.51 | 1.4 | 2.92 | 0.2 | -- | -- | -- | -- | -- | -- | -- |
| 22 | 28.7 | 7.65 | 1.0 | 1.57 | -- | -- | -- | -- | 0.1 | -- | -- | -- |
| 6 | 34.8 | 5.69 | 0.7 | -- | -- | 0.3 | -- | -- | -- | -- | -- | -- |
| Group totals | 28.5 | 4.41 | | | | | | | | | | |
| RES | | | | | | | | | | | | |
| 23 | 29.6 | 12.12 | 0.8 | 1.71 | e | 2.2 | -- | -- | 1.0 | -- | -- | 2.2 |
| 61 | 22.0 | 9.72 | 2.9 | 3.32 | m | 2.9 | -- | -- | -- | -- | -- | -- |
| 34 | 20.0 | 11.32 | 1.7 | 1.95 | g | 0.3 | -- | -- | -- | -- | -- | -- |
| | | | | | m | 0.1 | -- | -- | -- | -- | -- | -- |
| 56 | 21.6 | 9.01 | 0.6 | -- | m | 0.9 | -- | -- | -- | -- | -- | -- |
| 63 | 42.2 | 6.20 | 4.2 | 4.30 | | -- | 0.9 | -- | -- | 0.3 | -- | -- |
| 62 | 25.1 | | 0.5 | 1.2 | | -- | -- | -- | -- | 0.2 | -- | -- |
| 15 | 34.2 | 10.00 | 5.3 | 3.83 | e | 2.9 | 0.1 | -- | -- | -- | -- | -- |
| Group totals | 27.8 | 8.08 | | | | | | | | | | |

* m = *Picea mariana*
 g = *Picea glauca*
 e = *Picea engelmannii*

group. Although it might receive more than average precipitation, it occurs on a steep, plicated mountain slope made rugged by numerous water erosion channels. Tree regeneration has been slow, thus many parts of the site are not protected by forest cover and so dry out more quickly. When the stand with all of its topographic heterogeneity is taken as a single unit, it averages out as a mesic, high subalpine forest. However, when looked at closely, its similarity to the four Jasper representatives of this type, is less obvious.

6. *Shepherdia canadensis* type-SC (Stands 46-B, 36-B, 14-B, 50-B, 13-B, 20-J, 55-J, 52-J, 19-J)

This forest type occurs at middle elevations on terraces along valley walls and beside rivers. Surveyed Banff stands, of the type, occur within an altitudinal range of 400 feet (4800 - 5200 ft.); Jasper stands also occur within a 400 foot elevational range (3800 - 4200 ft.) (Figure 11). Since essentially the same forest type occurs in both areas, the difference of about 1000 feet in mean elevation between the two areas may represent the magnitude of elevational correction for latitude which should be made when equating specific vegetation zones in the two Parks (see also p. 59).

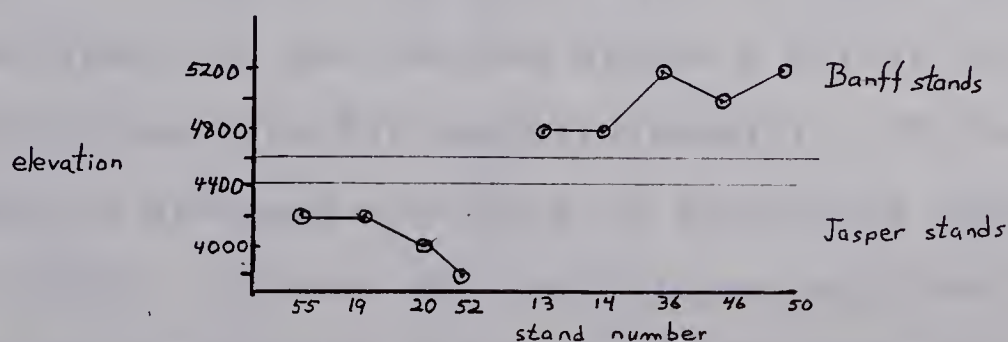


FIGURE 11. ELEVATION OF *SHEPHERDIA* TYPE STANDS.

With the exception of 19-J, the surveyed areas occurred on flat to gently sloping terrain (Table 5). The meso-phytic to moist appearance of the vegetation indicates that water is available in at least moderate amounts.

A well-developed high shrub stratum of *Shepherdia canadensis* characterizes this forest type. The high shrub stratum is generally not continuous or closed; rather, it consists of a widely distributed population of isolated and loosely aggregated individuals.

A gradient of available water may exist within this forest type. At one extreme are sites such as 46-B in which the understory is structurally dominated by plants with broad leaves (e.g. *Aster ciliolatus* and *Senecio aureus*) while at the other extreme are sites such as 52-J in which xeromorphic leaves are dominant (e.g. *Arctostaphylos uva-ursi*). Degrees of xeromorphy are often expressed within individual species (e.g. *Linnaea borealis* or *Elymus innovatus*); species which were in all stands of the type tended to have smaller, thicker leaves on the drier sites than on the moister sites.

The number of vascular species per stand is also higher in those stands with the more luxuriant understory (e.g. stands 46-B and 36-B). Species diversity might be indicative of the relative moistness of the habitat within a forest type (see p. 53 of the *Alnus* type for another example). If the stands of the type are arranged according to decreasing species diversity (Table 6) then the Banff representatives occur at one end (moister) while the Jasper group appears at the

TABLE 5. AGE AND MACROTOPOGRAPHY OF STANDS OF PRIMARY SURVEY

| | | Age | | | % Slope | | Exposure | Elevation Feet AMS. |
|-----|----|-------------|-------|----------|---------|-------|-------------|---------------------------|
| | | Pop. age | Range | Max. | Mean | Range | | |
| MG | 41 | 78.7 | 27 | 87 | 31 | 10-54 | SW | 6000 |
| | 42 | 67.3 | 32 | 75 | 11 | 3-26 | NW→N, SW→S | 5500 |
| | 40 | 42.3 | 38 | 70 | 9 | 2-22 | | 5500 |
| | X | 62.8 | | | 17.0 | | | 5650 |
| | Sx | 18.62 | | | 12.16 | | | 300 |
| | | | | | | | | |
| AC | 25 | 107.7 | 55 | 123 | 17 | 13-25 | NW→N→NE→ESE | 4100 |
| | 28 | 118.5 | 36 | 122 | 20 | 6-44 | SW→W→N→E→SE | 4100 |
| | 31 | 75.7 | 24 | 89 | 17 | 3-30 | E | 4700 |
| | 33 | 48.9 | 22 | 63 | 6 | 0-12 | E | 4100 |
| | X | 87.7 | | | 15.0 | | | 4250 |
| | Sx | 31.61 | | | 6.16 | | | 300 |
| FM | 26 | 107.3 | 46 | 136 | 6 | 0-25 | SE | 3800 |
| | 18 | 61.2 | 4 | 63 | 11 | 4-20 | S→E→NE | 4000 |
| | 17 | 42.2 | 27 | 237 | 10 | 0-38 | NE→SE, (W) | 4100 |
| | 7 | 118.1 | 36 | 122 | 9 | 1-20 | SW | 4750 |
| | 11 | 117.3 | 40 | 128 | 20 | 10-30 | N | 4900 |
| | 12 | 42.7 | 12 | 53 | 19 | 12-30 | N | 5000 |
| | 9 | 102.8 | 31 | 126 | 43 | 28-65 | N | 5400 |
| | 44 | 72.1 | 30 | 76(126) | 33 | 22-45 | N | 5600 |
| | 43 | 60.7 | 17 | 77 | 43 | 35-50 | NW | 5700 |
| | 48 | 108.5 | 49 | 116 | 19 | 5-55 | WSW-NW | 6000 |
| | 51 | 115.0 | 26 | 118 | 33 | 15-60 | NE | 4700 |
| | X | 86.2 | | | 22.4 | | | 4900 |
| | Sx | 30.55 | | | 13.54 | | | 750 |
| | | | | | | | | |
| VS | 47 | 62.6 | 18 | 68 | 3 | 2-6 | SW | 5800 |
| | 39 | 79.7 | 35 | 96 | 38 | 3-80 | WSW | 5400 |
| | 10 | 40.2 | 9 | 51 | 12 | 8-20 | E | 5200 |
| | 45 | 74.3 | 28 | 80 | 5 | 3-10 | E | 5000 |
| | X | 64.2 | | | 14.5 | | | 5350 |
| | Sx | 17.52 | | | 16.13 | | | 350 |
| MHS | 49 | 43.1 | 26 | 51 | 57 | 38-80 | NE | 5500 |
| | 57 | 63.3 | 9 | 137(316) | 35 | 20-55 | WSW | 6100 |
| | 58 | 79.3 | 6 | 83 | 29 | 22-38 | SW | 5800 |
| | 59 | 65.2 | 13 | 67 | 11 | 5-25 | NW | 5400 |
| | 60 | 51.7 | 22 | 60 | 22 | 11-35 | E | 5800 |
| | X | 60.5 | | | 30.8 | | | 5700 |
| | Sx | 13.82 | | | 17.15 | | | 300 |
| SC | 46 | 65.0 | 53 | 101 | 36 | 9-80 | E | 5000 |
| | 36 | 85.7 | 60 | 122 | 15 | 6-27 | SW | 5200 |
| | 14 | 50.7 | 31 | 62 | 8 | 1-35 | N→E | 4800 |
| | 50 | 101.6 | 23 | 110 | 36 | 7-75 | WSW | 5200 |
| | 13 | 59.7 | 34 | 72 | 15 | 0-40 | N | 4800 |
| | 20 | 60.8 | 19 | 65 | 17 | 0-52 | SE→S | 4000 |
| | 55 | 83.7 | 13 | 84 | 18 | 2-55 | SW | 4200 |
| | 52 | 67.3 | 52 | 90 | 8 | 0-18 | N | 3800 |
| | 19 | 58.2 | 25 | 67 | 31 | 12-61 | NE→E→SE | 4100 |
| | | | | | | | | |
| | | | | | | | | |

Table 5 concluded

| | | Age | | | % Slope | | Exposure | Elevation Feet AMS. |
|-----|----|-------------|--------|---------|---------|-------|------------|---------------------------|
| | | Pop. age | Range | Max. | Mean | Range | | |
| | 29 | 87.4 | 43 | 128 | 5 | 0-10 | SE | 4000 |
| | 5 | 85.3 | 20 | 86 | 9 | 6-12 | | 4800 |
| | X | 73.2 | | | 18.0 | | | 4550 |
| | Sx | 16.11 | | | 11.34 | | | 500 |
| AU | 1 | 59.5 | 83 | 144 | -- | -- | | 3500 |
| | 2 | 55.8 | 10 | 59 | -- | -- | | 3800 |
| | 3 | 61.7 | 6 | 65 | -- | -- | | 3700 |
| | 16 | 57.9 | 9 | 66 | 9 | 0-16 | SSE→E | 3800 |
| | 24 | 51.0 | 56 | 91 | 1 | 0-6 | | 3800 |
| | 27 | 59.6 | 37 | 90 | 11 | 0-28 | W→S→E | 3950 |
| | 30 | 53.2 | 41 | 93 | 8 | 2-15 | SE | 3900 |
| | 32 | 50.0 | 1 | 196 | 6 | 0-12 | | 3950 |
| | 35 | 68.5 | 2 | 70 | 4 | 0-12 | | 4800 |
| | X | 57.5 | | | 6.5 | | | 3900 |
| | Sx | 5.78 | | | 3.62 | | | 350 |
| EI | 38 | 69.1 | 48 | 110 | 4 | 0-6 | | 5000 |
| | 37 | 96.0 | 51 | 123 | 5 | 2-8 | ENE | 4900 |
| | 21 | 123.0 | 47 | 133 | 10 | 2-30 | S→E | 3800 |
| | 54 | 94.2 | 26 | 100 | 51 | 20-75 | SE | 4000 |
| | 53 | 37.3 | 5 | 92(227) | 24 | 8-55 | SE | 4000 |
| | 4 | 42.7 | 28 | 74 | 6 | 0-12 | SW | 4800 |
| | 8 | 96.8 | 18 | 99 | 22 | 8-55 | S | 4800 |
| | 22 | 79.2 | 12 | 84 | 46 | 22-70 | S | 4500 |
| | 6 | 60.5 | 10 | 106 | 14 | 3-28 | WSW | 5000 |
| | X | 77.6 | | | 20.2 | | | 4600 |
| | Sx | 28.0 | | | 17.6 | | | 450 |
| RES | 23 | 87.3 | 9 | 94 | 39 | 13-60 | SE→E, N→NW | 4200 |
| | 61 | 153.9 | 7(101) | 36(199) | 21 | 7-45 | SW→N | 4000 |
| | 34 | 56.5 | 18 | 61 | 20 | 12-32 | SW | 5400 |
| | 56 | 51.7 | 22 | 60 | 8 | 2-28 | | 4200 |
| | 63 | 52.2 | 30 | 74 | 18 | 8-30 | S | 5900 |
| | 62 | 24.4 | 60 | 77 | 20 | 5-44 | NNW-NE | 4200 |
| | 15 | 79.5 | 29 | 97 | 23 | 17-30 | WNW | 5200 |
| | X | 72.2 | | | 21.3 | | | 4650 |
| | Sx | 41.4 | | | 9.2 | | | 700 |

other (drier) end. This sequence tends to support the hypothesis (Stringer 1966) that Jasper has a more xeric environment than does Banff.

TABLE 6. SPECIES DIVERSITY OF STANDS OF THE *SHEPHERDIA* TYPE.

| Stand # | 46-B | 36-B | 14-B | 50-B | 29-J | 20-J | 55-J | 52-J | 19-J |
|-----------------------|------|------|------|------|------|------|------|------|------|
| # of vasc. species | 61 | 58 | 56 | 55 | 52 | 50 | 47 | 41 | 40 |

The effect that greater moisture has upon the vegetation is illustrated by stand 19-J. It is situated on a plicated, north facing slope of a hill north of Cabin Lake. In the low areas of the plications, both water and fine soil particles tend to collect. The fine soil aids in the holding of water for longer periods than is possible on the ridge tops; therefore, the low areas tend to be moister than the ridges. Herbaceous vegetation grows rank and species diversity is greater in the hollows than on the upper areas. Plants such as *Aquilegia flavescens*, *Viola rugulosa*, *Rubus pubescens*, and *Osmorhiza chilensis*, which are indicative of moister habitats, occur in the depressions but not on the ridges.

Stands 14-B and 36-B are quite similar with respect to their tree diameter size-class distributions (Figure 10). Both have a wide range of diameter size-classes and ages indicating that forest establishment has been relatively slow following fire. There is no direct evidence for ground fires in the two stands. That stand 14-B is denser and has a lower basal area than does stand 36-B may be due to the immaturity

of the former stand. Smithers (1961) indicates that pine forests in Alberta do not reach maximum basal areas until about 60 years; thus 14-B at 51 years may yet increase in basal area. The relative immaturity of 14-B is further indicated by the low mortality of pine. That mortality in 36-B is restricted to the smallest diameter class is indicative of the open nature of the pine forest throughout its development, such that intraspecific pine competition has been low for most trees.

Stands 46-B and 50-B are also similar to each other with respect to the pine population structure. They have a moderately wide range of tree diameters but less than in the previous two stands. The age distribution is of the same form as stands 14-B and 36-B but in 50-B its range is less, indicating that canopy closure occurred more quickly in the latter stand. The presence of young trees in the larger diameter classes indicates that trees are growing in aggregations with openings between clumps such that new individuals are able to become established free of competition and thus are able to attain larger diameters. The low mortality in 46-B as compared with 50-B may be indicative of immaturity due to slow forest establishment in the former.

There is no evidence of ground fires in the Banff stands of this forest type. Fire scars were not seen either on the tree trunks or in increment cores taken from the trees. Dead branches are present on the pine to within a foot of the ground - this is further evidence that ground fires probably

have not occurred here since the present forest became established.

The Jasper stands, though similar in most respects to those of Banff, also have interesting differences. All five of the Jasper representatives show a wide range of diameter size-classes and age groups. For stands 19-J and 20-J this would appear due to a slow regeneration of pine following fire. There is no evidence of ground fires after forest establishment. These two stands, although still immature in age (19-J 58 years, 20-J 61 years) and of moderate density, show fairly mature pine population profiles with respect to the frequency distribution of living and dead trees (Figure 10).

Stands 29-J and 52-J both show evidence of at least one ground fire about 30 years after initial forest establishment. It appears that the response of 29-J was to completely reseed the area following the fire and quickly bring the level of stocking up to its maximum. Pine mortality would indicate that this stand is rapidly approaching maturity. Stand 52-J on the other hand has low pine mortality and less than half the density of 29-J, thus indicating that regeneration has been much slower and the stand more open for most of its history.

Stand 55-J is unique amongst the modal *Shepherdia* type stands in that concomitant with its low density and moderately high precipitation is the lack of reproduction of the climax species *Abies* and *Picea*. This stand resembles a true

have not occurred here since the present forest became established.

The Jasper stands, though similar in most respects to those of Banff, also have interesting differences. All five of the Jasper representatives show a wide range of diameter size-classes and age groups. For stands 19-1 and 20-1 this would appear due to a slow regeneration of pine following fire. There is no evidence of ground fires after forest establishment. These two stands, although still immature in age (19-1 58 years, 20-1 61 years) and of moderate density, show fairly mature pine population profiles with respect to the frequency distribution of living and dead trees (Figure 10).

Stands 29-1 and 22-1 both show evidence of at least one ground fire about 50 years after initial forest establishment. It appears that the response of 29-1 was to completely reseed the area following the fire and quickly bring the level of stocking up to its maximum. Pine mortality would indicate that this stand is rapidly approaching maturity. Stand 22-1 on the other hand has low pine mortality and less than half the density of 29-1, thus indicating that regeneration has been much slower and the stand more open for most of its history.

Stand 25-1 is unique amongst the modal *Abies* type stands in that concomitant with its low density and moderately high precipitation is the lack of reproduction of the climax species *Abies* and *Picea*. This stand resembles a true

climax forest. See discussion of stand 55-I-J (p. 182) for a more complete account of this hypothesis.

Although the *Shepherdia* type is fairly well defined, it does grade into other forest types. For example, the cluster analysis (Figure 5) indicates that stands 29-J and 50-B were closely related to the cool moist forest group. This is primarily due to the high cover of feather mosses in these stands. Stand 18-J, described in the Feather moss type, has a large *Shepherdia* population. It is located within the elevational zone of this type in Jasper - only about one mile east of stand 20-J.

The Cluster analysis associates stand 5-B with the cool, moist *Shepherdia* forest type, but the stand lacks a well-developed *Shepherdia* stratum. It resembles stand 20-J but with a lower species diversity and a smaller population of *Shepherdia*.

Stand 13-B is linked to the *Shepherdia* type via 5-B in the cluster analysis. This is probably indicative of the moist habitat of these stands. The physiognomy and species composition of stand 13-B resembles that of stand 14-B - a close geographic neighbour. Stand 13-B is of moderate density (41) and has a wide range of tree diameters, but is relatively even-aged. Thus, together with the information from Figure 10 showing high mortality in the smallest diameter class, it appears that this stand is well on the way to differentiating into a moist *Shepherdia* forest type although its line of development is different from that

of the modal *Shepherdia* type.

7. *Elymus innovatus* type-EI (Stands 6-B, 22-J, 21-J, 37-B, 54-J, 4-B, 8-B, 38-B)

The *Elymus* type is probably transitional between the more xerophytic *Arctostaphylos* type and the more mesophytic *Shepherdia* type. Stands such as 4-B and 21-J are the best representatives of this type. Structurally they are quite simple: there is a tree stratum of average density, there is no shrub stratum, there is a very well-developed herb stratum dominated by *Elymus innovatus*, and bryophytes and lichens are not common enough to form a stratum as such.

All of the sampled stands of this type (except 22-J), fall within the elevational range of the *Shepherdia* type in their respective Parks. This may indicate the potential of either of these types to develop into the other if the environment changes. Support for this idea comes from stand 50-B of the *Shepherdia* type. In addition to a well-developed *Shepherdia* stratum, this stand has a herb stratum dominated by a lush growth of *Elymus innovatus*. The cluster analysis (Figure 6) links 50-B to the *Elymus* type, but I have placed the stand in the *Shepherdia* type because of its well-developed shrub stratum. Stand 29-J, which is linked to 50-B (Figure 6), has a more poorly developed *Shepherdia* stratum but a well-developed herb stratum of *Elymus*. These two stands then emphasize the gradient of variation which exists between the two forest types.

The two modal representatives of this type (stand 4-B

and 21-J) occur on fairly level, glacial till but the other representatives of the type occur on a wide variety of slopes which may be composed of till or tallus. Those stands which occur on steeper slopes tend to have an aspect of between 90° and 250° (Table 5), meaning a high incident solar radiation load and thus a potentially warmer and drier than average habitat.

The stands other than the two modal ones listed with this type all fit the nodal concept of the *Elymus* type less perfectly than the modal stands. These other stands represent mosaics of types (e.g. stands 6-B, 8-B and 37-B are a mosaics of Feather Moss, *Vaccinium scoparium* and *Elymus* types; and stands 22-J, 53-J and 54-J are mosaics of *Elymus*, *Alnus*, and *Arctostaphylos* types). Because of the vegetational diversity included in these mosaics, these stands do not strengthen the concept of the *Elymus* type; but rather, they again emphasize the degree to which this type intergrades into other forest types in the two Parks. In view of the heterogeneity of the *Elymus* type, it is apparent that further intensive study is required if the relationships of this type to other forest types are to be clearly understood.

C. XEROPHYTIC FOREST CLASS

8. *Arctostaphylos uva-ursi* type (stands 1-J, 2-J, 3-J, 16-J, 24-J, 27-J, 30-J, 32-J, 35-B)

These stands occur in the warm, dry, low valley-bottoms. Stands 3-J and 16-J are exceptions in that they occur on low

benches on the Athabasca River Valley wall. All the stands except 2-J, 3-J and 16-J occur on flat to gently sloping terrain such as river terraces. These latter three stands are all within close proximity of one another and occur on tops of knolls or their lower slopes as in 3-J.

Vegetationally these stands are characterized by a low species diversity and sparse populations of those which are present, with the exception of *Arctostaphylos uva-ursi*, *Linnaea borealis*, and *Elymus innovatus*. The former two species occur in large scattered aggregations with the *Linnaea* tending to occupy more shaded, cooler, and moister sites than the *Arctostaphylos*. The *Elymus* exhibits a much less pronounced pattern although it is more abundant in areas of moderate canopy density and less common in both large openings and sites with a locally high tree density. *Vaccinium vitis-idaea* occurs sporadically in small depressions. *Shepherdia canadensis* and *Juniperus communis* both occur throughout these forests but their development is quite poor - individual plants tend to be either small and lacking in vigour or if larger and healthier then few in numbers. Stand 27-J, which occurs in an area of poor drainage and thus is probably slightly moister, has a larger *Shepherdia* population indicating that these dry forests have the potential to develop into *Shepherdia* forest types if conditions became wetter.

These forests are all between 50 and 70 years old and appear to be of fire origin (indicating the occurrence of

numerous fires in the low valley bottoms between 1900 and 1920). In contrast to those of the *Shepherdia* Forest type, stands of the *Arctostaphylos* forest type (exceptions 24-J and 32-J) all rapidly regenerated a pine forest following fire. The pine population structures as indicated in Figure 10 show relatively even-aged populations of trees with narrow ranges of diameters.

Tree mortality is quite variable between sites, being lowest in both the most and the least dense stands and moderate in the stands of intermediate density. Stand 3-J despite its high living density (115) has considerable standing dead pine.

The fact that most of these stands could have fairly large quantities of potentially available water in the upper 5 - 15 cm. of mineral soil, (15-30% excluding stand 1-J) does not appear to be an important factor, as these sites probably only rarely have saturated soil. The small amount of precipitation received plus the warm summer temperatures appear to be the most important limiting factors in stand differentiation.

A more detailed account of the structure and variability to be found in forests of this type may be found in the discussion of intensive stand 24-J-I (p.201).

Forests of this type show the fewest signs of being succeeded by *Picea glauca* or *Abies lasiocarpa*. Reproduction of these species is poor, and in the case of *Abies* seedlings which become established, they are severely

browsed by elk. *Pseudotsuga* seedlings were exceedingly rare. Under the present Parks policy of fire control, natural rejuvenation of these pine forests, which follows fire, is greatly inhibited. Thus one could expect the present forests to continue as a type of climax forest which at most might become mixed-coniferous in composition.

Of all the pine forest types in the two Parks, this and the *Elymus* type are probably the most utilized by large herbivores. These sites form part of the summer and winter ranges of both elk and deer. Fairly large herds of elk were often seen browsing here, and numerous trails are to be found throughout the area.

Man's use of these forests is similar to that of the *Shepherdia* type. Parts of campgrounds such as Wapiti and Wabasso occupy this forest type. Stand 1-J is traversed by several riding trails associated with Jasper Park Lodge.

9. Residual stands (23-J, 61-J, 8-B, 34-J, 56-J, 63-J, 62-B)

This section relates the remaining stands to the classification system proposed.

Due to a lack of field experience during the first summer, several of the surveyed stands encompass habitat diversity which is greater than that upon which the proposed classification of forest types is based. Thus stands 23-J and 61-J are associated with the cool, moist forest because of an abundance of feather mosses over a portion of their area. But they have affinities to the more mesic forests

because of more open, dry areas with little moss cover and greater grass and *Arctostaphylos* cover plus *Juniperus communis* and *Shepherdia*. Stand 23-J is heterogeneous because it includes both a dry southeast exposure and a moist protected northwest exposure. Stand 61-J is heterogeneous because of irregular topography and a mosaic of vegetation resulting from at least three spotty ground fires. Stand 8-B is similar to 61-J and 23-J (see cluster analysis Figure 6). It includes a low, flat, moist river-terrace plus a dry exposed knoll. The low area is similar to the Feather Moss Forests with a little more *Shepherdia* than the typical forests. The drier area is like the *Shepherdia* forest type.

Stand 34-J is most closely associated with the mesic high subalpine forest. It differs from them in that it is dissected by several large, corridor-like clearings which are very wet (note the abundance of *Arctostaphylos rubra*). These clearings are probably avalanche chutes and thus permanently treeless; they should not have been included within the stand.

Stand 56-J is allied to the *Arctostaphylos* type but differs from it in that it consists of a mosaic of two forests of two ages which resulted from an irregular fire. The old areas are dense, have a developing *Picea mariana* understory and a dense feather moss carpet. The young areas are variable - from bare soil to *Arctostaphylos* mats or *Vaccinium caespitosum* mats.

Stand 63-J is also related to the *Arctostaphylos* type.

Like this type and stand 56-J it is quite young - 52 years. It is very variable in density as a result of irregular regeneration. The stand is a mosaic of moisture régimes from moist areas where vegetation is lush including a moss carpet with *Rhytidiadelphus triquetrus* to dry areas of sparse vegetation where *Peltigera canina* is quite abundant.

At present stand 62-B resembles the *Arctostaphylos* type, but because of its very young age - 24 years - it is difficult to classify. It is very unevenly stocked and thus presents a great diversity of habitats from open dry forest to cool moist forest. If succession to *Picea* and *Abies* is not too rapid (regeneration of these species is good in localized areas) a *Shepherdia* forest type could result.

Stand 6-B is peripherally associated with the *Shepherdia* type forest. It is heterogeneous in that it has locally moist depressions with species such as *Pyrola asarifolia*, *Moneses uniflora*, *Senecio aureus*, and *Senecio hydrophiloides* as well as large, drier areas with *Shepherdia canadensis* and *Arctostaphylos uva-ursi*. It differs from other *Shepherdia* types in that its pine population is relatively even-aged and has a narrow range of diameters.

The last surveyed area to be accounted for is stand 15-B. It resembles a poorly developed *Vaccinium* type forest. It is a fairly dense stand dissected by areas of poorly developed intermittent streams where *Picea* and feather mosses are more abundant. Despite its age of 80 years, it has a high

density (112) which may be retarding its development and differentiation.

X. INTENSIVE STUDY

A. INTRODUCTION

Having determined the major forest types present in the Primary Survey of the *Pinus contorta* vegetation of Banff and Jasper, it was thought desirable to study in detail as many of these types as time would allow. Thus during the summer of 1967, five of the types were studied:

- (1) *Menziesia glabella* type - stand 41-B-I,
- (2) A type intermediate between the moist *Vaccinium scoparium* and the *Shepherdia canadensis* type - stand 47-B-I,
- (3) low elevation Feather Moss type - stand 26-J-I,
- (4) *Shepherdia canadensis* type - stand 55-J-I,
- (5) *Arctostaphylos uva-ursi* type - stand 24-J-I.

The objectives of the detailed study were:

- (1) to determine the distribution patterns of species within a square, one hectare area in each of five pine forest types which were subjectively thought to be as topographically uniform as could be found in the Parks;
- (2) to relate species distribution patterns within each stand to the microtopography of the stand;
- (3) to determine interspecific correlations of species distributions (e.g. the relationship between understory species distributions and the distribution of the species in the tree stratum);

- (4) to obtain detailed information about the pine tree population structures, i.e. age, height, crown depth, diameter and density distributions;
- (5) to obtain a first approximation of the spatial variability of soil nutrients within pine stands in the Parks.

B. LOCATIONS OF STANDS

The geographic locations of the five stands are given in Table 7 . The locations of the stands on aerial photographs are given in Appendix 4 . A description of the topography of the stand and surrounding land, and the relationship of the stands to geographic features such as roads are given below.

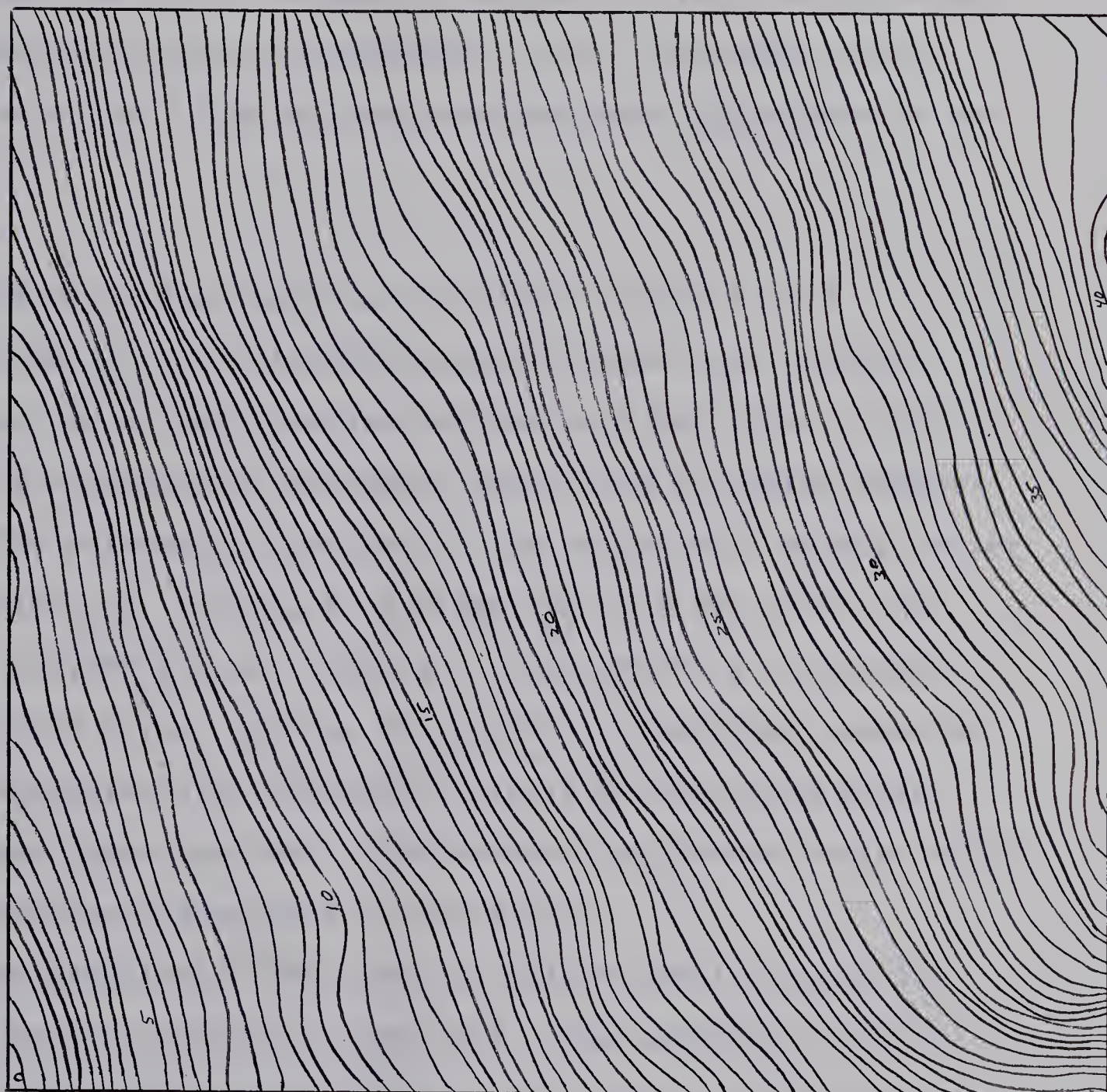
TABLE 7. LOCATIONS OF INTENSIVE STANDS

| <u>Stand No.</u> | <u>N. latitude</u> | <u>W. longitude</u> |
|------------------|--------------------|---------------------|
| 41-B-I | 51° 31' | 116° 15' |
| 47-B-I | 50° 55' | 115° 24' |
| 26-J-I | 53° 43' | 117° 56' |
| 55-J-I | 52° 34' | 117° 43' |
| 24-J-I | 52° 45' | 117° 58' |

The *Menziesia* type (MG): stand 41-B-I

Stand 41-B-I is situated at approximately 6,100 ft (1,860 m) on the southwest slope of Mt. Hector (ca. 11,000 ft) above Highway 93 about 5.6 miles north of its junction with Trans Canada Highway No.1. The stand is located on a steep slope (ca. 25°) in contrast to the relatively level nature of the other intensively studied stands (Figure 12).

FIGURE 12. TOPOGRAPHY OF INTENSIVE STAND 41-B-I,
contour interval = 50 cm
elevations are relative



N
↑

The slope of the stand is topographically quite uniform with the major exception of the southeast corner which dips into a steep-sided ravine.

This stand is situated in the upper subalpine *Picea-Abies* zone, and the forests around it and up to tree line are mixed coniferous i.e. *Picea engelmannii*, *Abies lasiocarpa*, and *Pinus contorta*. Pine becomes more abundant lower down in the valley.

The *Vaccinium scoparium* type (VS): stand 47-B-I

Stand 47-B-I is located about 25 miles outh of Banff townsite, on a small plateau (elevation 5,800 ft, *ca.* 1,800 m) near the emergence of the Spray River from the Spray Reservoir. The plateau is situated at the bottom of a narrow valley (4.5 miles, *ca.* 7.2 km, from ridge top to ridge top). Mt. Nestor (10,000 ft, *ca.* 3,200 m) is to the NE and Turbulent Mtn. (9,000 ft, *ca.* 2,700 m) is to the W. The lower slopes of these mountains are covered by forests of *Picea* and *Abies* with some *Pinus contorta*. The numerous avalanche chutes which are present are dominated by *Salix* spp.

Topographically the stand is fairly level (Figure 13) with a maximum relief of about 1 m. The northeast corner of the stand comes within 50 m of the edge of the plateau.

The Feather Moss type (FM): stand 26-J-I

Stand 26-J-I (elevation 3,800 ft, *ca.* 1,200 m) is located on two terraces on the east side of the Whirlpool River about

FIGURE 13. TOPOGRAPHY OF INTENSIVE STAND 47-B-I.

contour interval = 10 cm

elevations are relative



one mile from its confluence with the Athabasca River. The area is triangular in shape being bounded by steeply rising hills on the south and east, and by the Whirlpool River on the west. The lower terrace is essentially flat while the upper one is undulating and has large rock outcrops (none of which occur in the stand). The major topographic feature of the upper terrace is a shallow depression leading towards the N (see Figure 14). At the river's edge, the lower terrace is about $\frac{1}{2}$ m above the summer water level.

The vegetation of the area surrounding the stand is dominated by *Pinus contorta*. Several, small, marl lakes to the south are surrounded by *Picea mariana*, while *Picea glauca/engelmannii* and *Abies lasiocarpa* occur sporadically in the immediate vicinity.

The Dry *Shepherdia* type (SC): stand 55-J-I

Stand 55-J-I (elevation 4,200 ft, *ca.* 1,300 m) is located southeast of Highway 93, one mile NW of the turnoff to Honey-moon Lake Campground in Jasper. It is on the uppermost terrace of the Sunwapta River and about 200 m from the base of the valley wall. There are no major topographic discontinuities within the stand (Figure 15), but the western half is flat with areas of exposed gravel, whereas the eastern half is hummocky. The hummocks vary in size with the largest being about 50 cm high and about 2 m long. Many hummocks (especially in the eastern portion of the area) contain few rocks but lie on top of a very gravelly base.

FIGURE 14. TOPOGRAPHY OF INTENSIVE STAND 26-J-1.

contour interval = 10 cm

elevations are relative

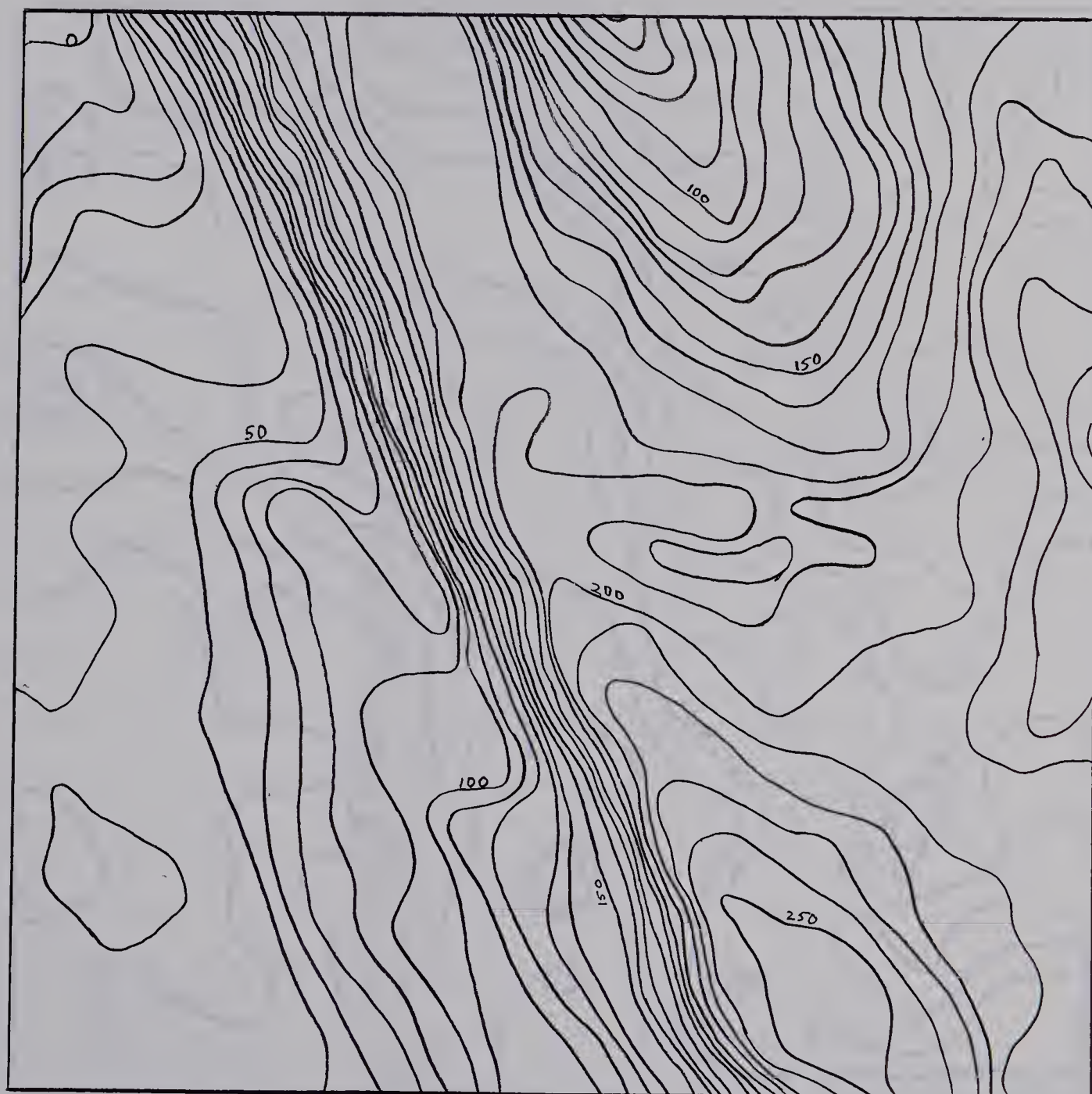
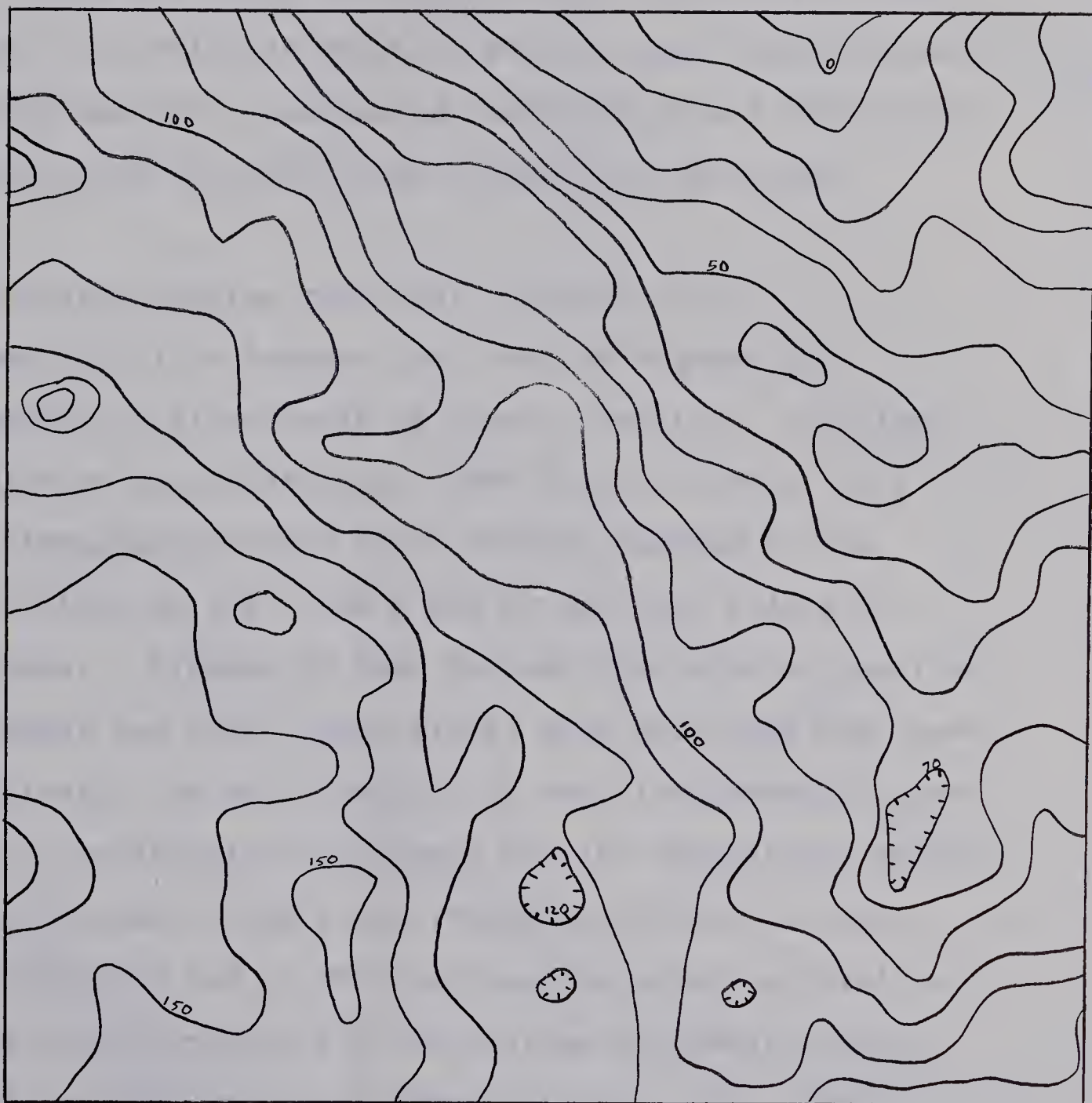


FIGURE 15. TOPOGRAPHY OF INTENSIVE STAND 55-J-1.

contour interval = 10 cm

elevations are relative



Examination of several hummocks showed that the soil horizons were either inverted, or very irregular and often lay on top of a "normal" profile (see p. 258).

The vegetation around this stand is predominantly pine forest. There are areas of *Picea mariana* surrounding lakes which are 1 - 2 miles to the E as well as some *Picea glauca/engelmannii* and *Abies lasiocarpa* scattered thinly throughout the lower valley forests in the vicinity of the stand.

The *Arctostaphylos* type (AU): stand 24-J-I

Stand 24-J-I is located just west of Highway 93 approximately 12 miles south of Jasper townsite. The stand is situated at an elevation of 3,800 ft, (ca. 1,200 m) on a large, triangularly-shaped river terrace bounded by the Athabasca River on the S and W and by low rock ridges on the northeast. Highway 93 cuts through the northeast section of the forest and three large gravel pits have been dug there. Topographically the area consists of two river terraces each of which is relatively flat except for low undulations which resemble old dunes. The stand itself lies about one mile from the northern end of this terrace and occurs entirely on the upper terrace except for the extreme southwest corner. The stand includes one major "dune" (Figure 16). These "dunes" may actually be old river islands and not wind deposits.

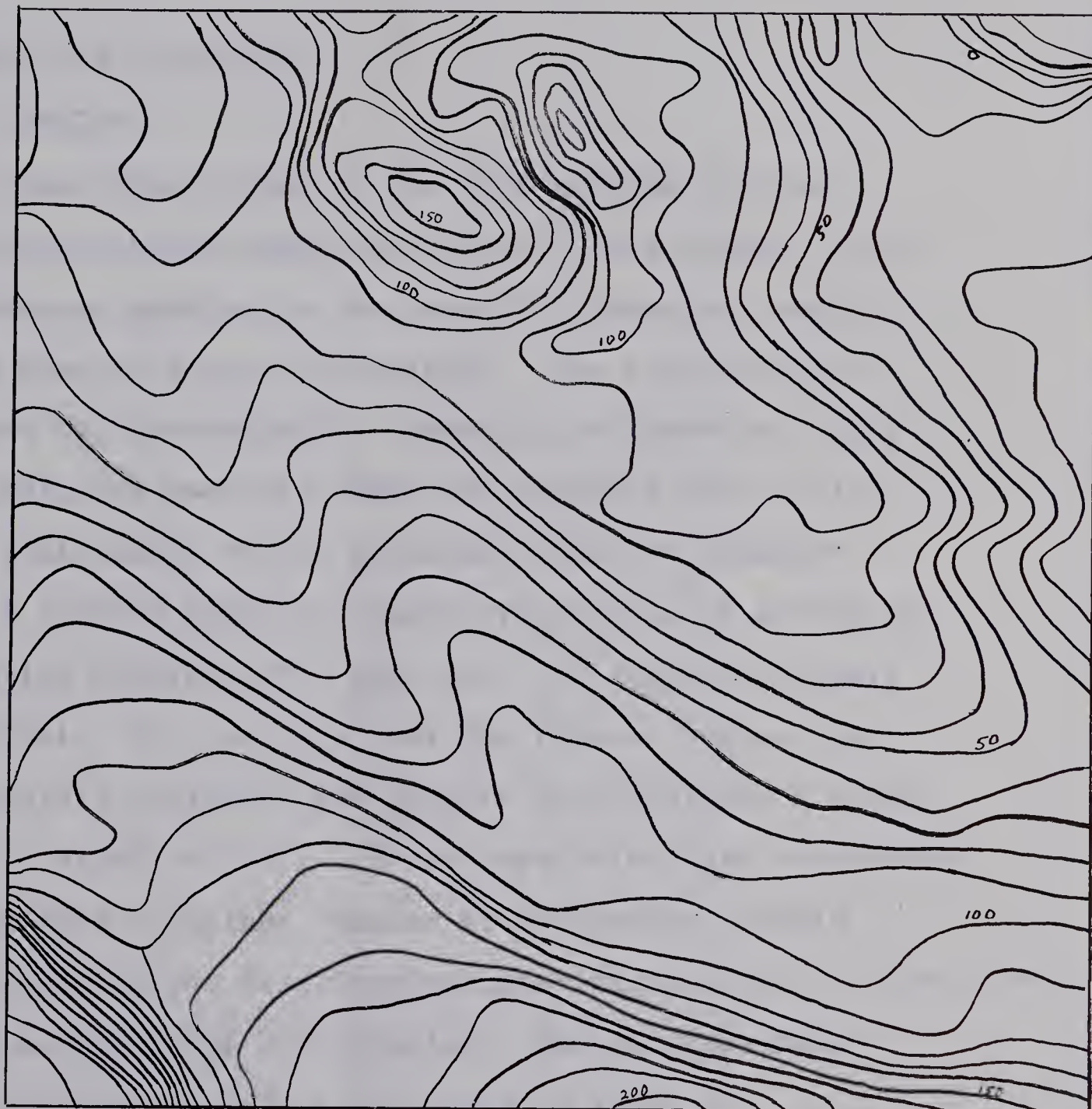
Pinus contorta dominates the very xerophytic wooded vegetation on alluvial deposits surrounding this stand;

FIGURE 16.

TOPOGRAPHY OF INTENSIVE STAND 24-J-I.

contour interval = 10 cm

elevations are relative



N



Pseudotsuga menziesii dominates the rocky ridges to the northeast. Many of the forests in this region of the Athabasca Valley are vegetationally even more poorly developed than is stand 24-J-I.

C. POPULATION STRUCTURE

1. TREE STRATUM

The individual trees of the tree stratum form non-randomly distributed populations in all five stands. This non-randomness applies to the pines by themselves and to all tree species taken collectively. The state of non-randomness was determined by comparing, by means of a Chi-square test, the observed number of quadrats with 0, 1, 2, ..., n individuals to the expected number of quadrats. (Table 8) based upon calculated frequencies of a Poisson distribution (Kershaw 1964 chp. 6). The large Chi-square values (Table 9) indicate that the Poisson series does not adequately represent the density distribution of trees (except in stand 26-J-I). If the populations are non-random, then they must be either regular or contagious. Field observations and the distribution maps (Figures 22, 49, 136, 179) indicate a contagious distribution. The variance:mean ratios (Greig-Smith 1957 p.62) shown in Table 9, confirm the contagious distributions (i.e. ratios greater than 1) in all cases except for the pine trees in stand 26-J-I.

Stand 26-J-I is of special interest because the pine

TABLE 8. THE OBSERVED AND EXPECTED NUMBER OF QUADRATS CONTAINING 0, 1, 2, ..., n INDIVIDUALS
DATA REFERS TO THE FIVE INTENSIVE STANDS.

| No. of individuals | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|--------------------|-------------------------|-----|-----|-----|----|----|----|----|----|-----|-----|----|----|----|----|----|-----|-----|----|----|----|
| 41-B-I | <i>Pinus</i> - expected | 0.1 | 1 | 4 | 12 | 23 | 37 | 49 | 56 | 56 | 49 | 39 | 28 | 19 | 11 | 6 | 3 | 2 | 1 | 0 | 0 |
| | observed | 10 | 4 | 13 | 28 | 29 | 35 | 32 | 41 | 48 | 44 | 25 | 24 | 16 | 15 | 12 | 6 | 6 | 4 | 3 | 1 |
| | all tree spp. ex. | 0.1 | 0.6 | 2 | 7 | 16 | 27 | 40 | 50 | 54 | 53 | 46 | 37 | 27 | 18 | 11 | 6 | 3 | 1 | 0 | 0 |
| | ob. | 7 | 1 | 8 | 20 | 27 | 27 | 29 | 40 | 61 | 46 | 30 | 28 | 15 | 24 | 13 | 6 | 7 | 5 | 3 | 1 |
| 47-B-I | <i>Pinus</i> - expected | 0.1 | 0.4 | 2 | 6 | 13 | 24 | 36 | 47 | 53 | 53 | 48 | 39 | 30 | 20 | 13 | 8 | 4 | 0 | 0 | 0 |
| | observed | 1 | 9 | 12 | 16 | 23 | 30 | 29 | 35 | 36 | 38 | 32 | 33 | 25 | 21 | 15 | 17 | 5 | 4 | 7 | 3 |
| | all tree spp. ex. | 0.0 | 0.2 | 1 | 4 | 9 | 18 | 28 | 36 | 44 | 48 | 48 | 40 | 32 | 24 | 16 | 8 | 0 | 0 | 0 | 0 |
| | ob. | 1 | 4 | 10 | 15 | 14 | 29 | 26 | 34 | 38 | 32 | 35 | 37 | 27 | 22 | 22 | 18 | 10 | 7 | 7 | 4 |
| 26-J-I | <i>Pinus</i> - expected | 26 | 71 | 97 | 88 | 60 | 32 | 15 | 6 | 2 | | | | | | | | | | | |
| | observed | 24 | 62 | 98 | 89 | 65 | 34 | 12 | 5 | 1 | | | | | | | | | | | |
| | all tree spp. ex. | 13 | 44 | 76 | 87 | 74 | 51 | 29 | 14 | 6 | 2 | | | | | | | | | | |
| | ob. | 18 | 46 | 86 | 78 | 60 | 55 | 26 | 19 | 5 | 7 | | | | | | | | | | |
| 55-J-I | <i>Pinus</i> - expected | 61 | 112 | 103 | 64 | 30 | 11 | 3 | 1 | 0.2 | 0.1 | | | | | | | | | | |
| | observed | 108 | 115 | 64 | 46 | 31 | 13 | 8 | 6 | 4 | 4 | 1 | | | | | | | | | |
| 24-J-I | <i>Pinus</i> - expected | 0.8 | 5 | 16 | 40 | 49 | 59 | 50 | 53 | 40 | 27 | 17 | 9 | 5 | 2 | 1 | 0.4 | 0.1 | 0 | 0 | 0 |
| | observed | 22 | 34 | 35 | 52 | 26 | 28 | 17 | 27 | 20 | 15 | 19 | 21 | 11 | 8 | 8 | 6 | 12 | 8 | 25 | |
| | all tree spp. ex. | 0.8 | 5 | 16 | 32 | 48 | 58 | 58 | 50 | 38 | 25 | 15 | 8 | 4 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| | ob. | 22 | 36 | 37 | 53 | 26 | 28 | 17 | 27 | 20 | 15 | 19 | 21 | 11 | 8 | 8 | 6 | 12 | 8 | 25 | |

TABLE 9. CHI-SQUARE TEST RESULTS FOR OBSERVED AND EXPECTED FREQUENCIES
IN TABLE 8, ALSO VARIANCE: MEAN RATIOS FOR TREE DISTRIBUTIONS.

| Stand | Chi-square | Critical 5% value | Degrees of freedom | Sx^2/\bar{x} |
|--------|---------------------------|-------------------------------|--------------------|----------------|
| 41-B-I | <i>Pinus</i> all trees | 708 708 | 26.3 26.3 | 16 16 |
| | | | | 2.2 1.9 |
| 47-B-I | <i>Pinus</i> all trees | 268 1.15 x 10 ⁶ | 26.3 30.1 | 16 19 |
| | | | | 2.2 2.1 |
| 26-J-I | <i>Pinus</i> all trees | 2.1 15.8 | 14.1 15.5 | 7 8 |
| | | | | 0.9 1.2 |
| 55-J-I | <i>Pinus</i> | 2381 | 14.1 | 7 |
| | | | | 2.0 |
| 24-J-I | <i>Pinus</i> all trees | 292 1972 | 25.0 25.0 | 15 15 |
| | | | | 4.7 |

tree density distribution is adequately approximated at the 5% level of significance by the Poisson series. This means the pine tree population could be randomly distributed but not necessarily as Cottam, Curtis, and Hale (1953) point out. A Chi-square test of geographic homogeneity (*ibid.*) (Chi-square = 54.8, d.f. = 23) indicates that the population is not randomly distributed. From the distribution map of the pine population (Figure 105) it is apparent that the pine density is higher on the west side of the plot and decreases eastward, therefore indicating a contagious distribution (see p. 166).

The densities of trees (by species) per hectare and per 5 x 5 m quadrat are given in Table 10. Stand 47-B-I has the highest density, the highest basal area (Table 10) and is the youngest of the five stands. Stand 41-B-I is the next highest in basal area and its density is proportionately less than that of 47-B-I. Stand 41-B-I is 1.4 times older than 47-B-I but the former has only 14% of the standing dead wood that the latter has. The difference in the amount of standing deadwood from these stands is not accountable by differing rates of fall of dead trees; rather, it seems that the greater mortality in 47-B-I is attributable to its denser initial stocking.

Stand 24-J-I has about the same density as 41-B-I but less than half the basal area and nearly 10 times the mortality of the latter. That the trees of 24-J-I are very contagiously distributed as compared with those of 41-B-I

TABLE 10. SOME QUANTITATIVE FEATURES OF THE TREE STRATA OF THE FIVE INTENSIVE STANDS.

| | 41-B-I | | 47-B-I | | 26-J-I | | 55-J-I | | 24-J-I | |
|---------------------------------|--------------------------------------|-----------------|---------------|----------------|---------------|----------------|-------------|-------|----------------|----------------|
| | \bar{X} | Sx | \bar{X} | Sx | \bar{X} | Sx | \bar{X} | Sx | \bar{X} | Sx |
| | Density (# of stems) | | | | | | | | | |
| | /H | /5x5m | /H | /5x5m | /H | /5x5m | /H | /5x5m | /H | /5x5m |
| <i>Pinus contorta</i> | (129) 2588 | 6.47 | (913) 3647 | 9.12 | (399) 966 | 2.42 | (36) 759 | 1.90 | (1197) 2764 | 6.91 |
| <i>Picea glauca/engelmannii</i> | 192 | 0.48 | 253 | 0.63 | 4 | 0.01 | -- | -- | 1 | 0.00 |
| <i>Picea mariana</i> | -- | -- | -- | -- | (13) 240 | 0.60 | -- | -- | 4 | 0.01 |
| <i>Populus tremuloides</i> | -- | -- | -- | -- | 17 | 0.04 | -- | -- | -- | -- |
| <i>Abies lasiocarpa</i> | 50 2830 | 0.13 7.08 | 1 3900 | -- | -- | -- | -- | -- | -- | -- |
| | | | | 9.75 | 1227 | 3.07 | 759 | 1.90 | 2769 | 6.92 |
| | Basal Area (m ² /hectare) | | | | | | | | | |
| <i>Pinus contorta</i> | (0.9) 34.9 | (1.84) 12.63 | (1.6) 39.9 | (2.53) 9.41 | (6.2) 25.7 | (3.90) 5.05 | (0) 16.5 | 5.05 | (2.1) 16.8 | (4.36) 7.81 |
| <i>Picea glauca/engelmannii</i> | 1.6 | -- | 0.5 | -- | -- | -- | -- | -- | -- | -- |
| <i>Picea mariana</i> | -- | -- | -- | -- | 1.5 | -- | -- | -- | -- | -- |
| <i>Populus tremuloides</i> | -- | -- | -- | -- | (0.1) 0.2 | -- | -- | -- | -- | -- |
| <i>Abies lasiocarpa</i> | (0.1) 0.3 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| | | | | | | | | | | |
| | Height (m) | | | | | | | | | |
| <i>Pinus contorta</i> | 13.7 | 3.23 | 13.5 | 2.88 | 22.1 | 2.88 | 21.3 | 4.04 | 10.2 | 4.17 |
| <i>Picea glauca/engelmannii</i> | ? | ? | 9.6 | -- | 5.0 | -- | -- | -- | -- | -- |
| <i>Picea mariana</i> | -- | -- | -- | -- | 14.2 | -- | -- | -- | -- | -- |
| <i>Populus tremuloides</i> | -- | -- | -- | -- | -- | ? | -- | -- | -- | -- |
| <i>Abies lasiocarpa</i> | 17.8 | -- | -- | -- | -- | -- | -- | -- | -- | -- |

TABLE 10. Cont'd.

| | 41-B-I | | 47-B-I | | 26-J-I | | 55-J-I | | 24-J-I | |
|---------------------------------|-----------|-------|-----------|-------|----------------|-------|-----------|-------|-----------|-------|
| | \bar{X} | Sx | \bar{X} | Sx | \bar{X} | Sx | \bar{X} | Sx | \bar{X} | Sx |
| | /H | /5x5m | /H | /5x5m | DBH (cm) /H | /5x5m | /H | /5x5m | /H | /5x5m |
| <i>Pinus contorta</i> | 13.6 | 4.90 | 12.9 | 4.93 | 21.0 | 6.15 | 24.1 | 7.77 | 11.4 | 7.37 |
| <i>Picea glauca/engelmannii</i> | 7.6 | -- | 7.1 | -- | 6.3 | -- | -- | -- | -- | -- |
| <i>Picea mariana</i> | -- | -- | -- | -- | 13.5 | -- | -- | -- | 7.6 | -- |
| <i>Populus tremuloides</i> | -- | -- | -- | -- | 15.2 | -- | -- | -- | -- | -- |
| <i>Abies lasiocarpa</i> | 7.6 | -- | 6.1 | -- | -- | -- | -- | -- | -- | -- |
| Crown Depth (m) | | | | | | | | | | |
| <i>Pinus contorta</i> | 7.4 | 3.66 | 5.9 | 2.74 | 10.1 | 4.48 | 16.4 | 4.57 | 6.6 | 4.30 |
| <i>Picea glauca/engelmannii</i> | -- | -- | 8.2 | -- | -- | -- | -- | -- | -- | -- |
| <i>Picea mariana</i> | -- | -- | -- | -- | 12.4 | -- | -- | -- | -- | -- |
| <i>Populus tremuloides</i> | -- | -- | -- | -- | ? | ? | -- | -- | -- | -- |
| <i>Abies lasiocarpa</i> | 12.8 | -- | ? | ? | -- | -- | -- | -- | -- | -- |
| % Cover | | | | | | | | | | |
| <i>Pinus contorta</i> | 53.7 | -- | 44.6 | -- | 40.0 | -- | 18.1 | -- | 39.5 | -- |
| <i>Picea glauca/engelmannii</i> | 2.3 | -- | 2.5 | -- | -- | -- | -- | -- | -- | -- |
| <i>Picea mariana</i> | -- | -- | -- | -- | 6.32 | -- | -- | -- | 0.08 | -- |
| <i>Populus tremuloides</i> | -- | -- | 0.12 | -- | 1.64 | -- | -- | -- | 0.08 | -- |
| <i>Abies lasiocarpa</i> | 0.12 | -- | 0.04 | -- | -- | -- | -- | -- | -- | -- |

is indicative of the reason for the disparity in mortality and basal area between the two stands. Mortality is negligible in the open areas of 24-J-I but very high in the densely-stocked areas. The stand is in a very xeric area as opposed to the moist area of stand 41-B-I. Since available water is a major limiting factor in the Parks, the moisture difference could account for the productivity difference (as estimated from basal area) between the stands.

Stands 26-J-I and 55-J-I have the lowest densities and lowest basal areas of the five stands. Stand 26-J-I is also the oldest of the five and has a large number of standing dead trees despite its low density. It appears that this forest has passed maturity and begun to break up.

The mean height, diameter, and photosynthetic crown depth of the pine trees (Table 10) are controlled in part by the potential productivity of the site and by the tree density. If the stands are ranked according to increasing crown depths (47-B-I, 24-J-I, 41-B-I, 26-J-I, 55-J-I) the resulting series parallels the stand series of decreasing density. This is not unexpected considering the low shade tolerance of living pine needles. The modifying effect of site potential, in addition to density effects, is more evident in the diameter and height growth of the pine than in the crown depths. The stands, ranked according to increasing tree height, show the xerophytic stand, 24-J-I, with the lowest mean height, then the densest stand, 47-B-I followed by the dense stand 41-B-I.

The two most open stands, which had the deepest crowns also have the tallest trees, but the moister site, 26-J-I, has taller trees than the warmer, drier site 55-J-I. The rank order of the stands according to mean DBH is similar to that for height with the exception that stand 55-J-I has a greater mean DBH than stand 26-J-I.

The percent cover of pine (determined from the 2,500 cover points, see p.22) is lowest in the least dense stand (55-J-I) and highest in the second most dense stand (41-J-I). The percent cover of stand 24-J-I and 26-J-I is nearly identical while that of 47-B-I is slightly higher.

The mean ages of the five Intensive Stands (Table 11) do not correlate well with the six attributes of the tree stratum discussed above. The effects of tree density and potential productivity of the sites appears to completely obscure any inter-stand differences due to age.

TABLE 11. AGES OF INTENSIVE STANDS

| <u>Stand No.</u> | <u>Mean Age</u> | <u>S.D.</u> |
|------------------|-----------------|-------------|
| 41-B-I | 81.5 | 7.71 |
| 47-B-I | 58.2 | 6.46 |
| 26-J-I | 129.4 | 9.02 |
| 55-J-I | 74.5 | 18.53 |
| 24-J-I | 61.8 | 19.47 |

The frequency distributions of density in DBH classes (Figure 17) indicates that stand 41-B-I and 47-B-I are similar in that pine reproduction is negligible. *Picea engelmannii* appears to be slowly invading the stands. *Abies*

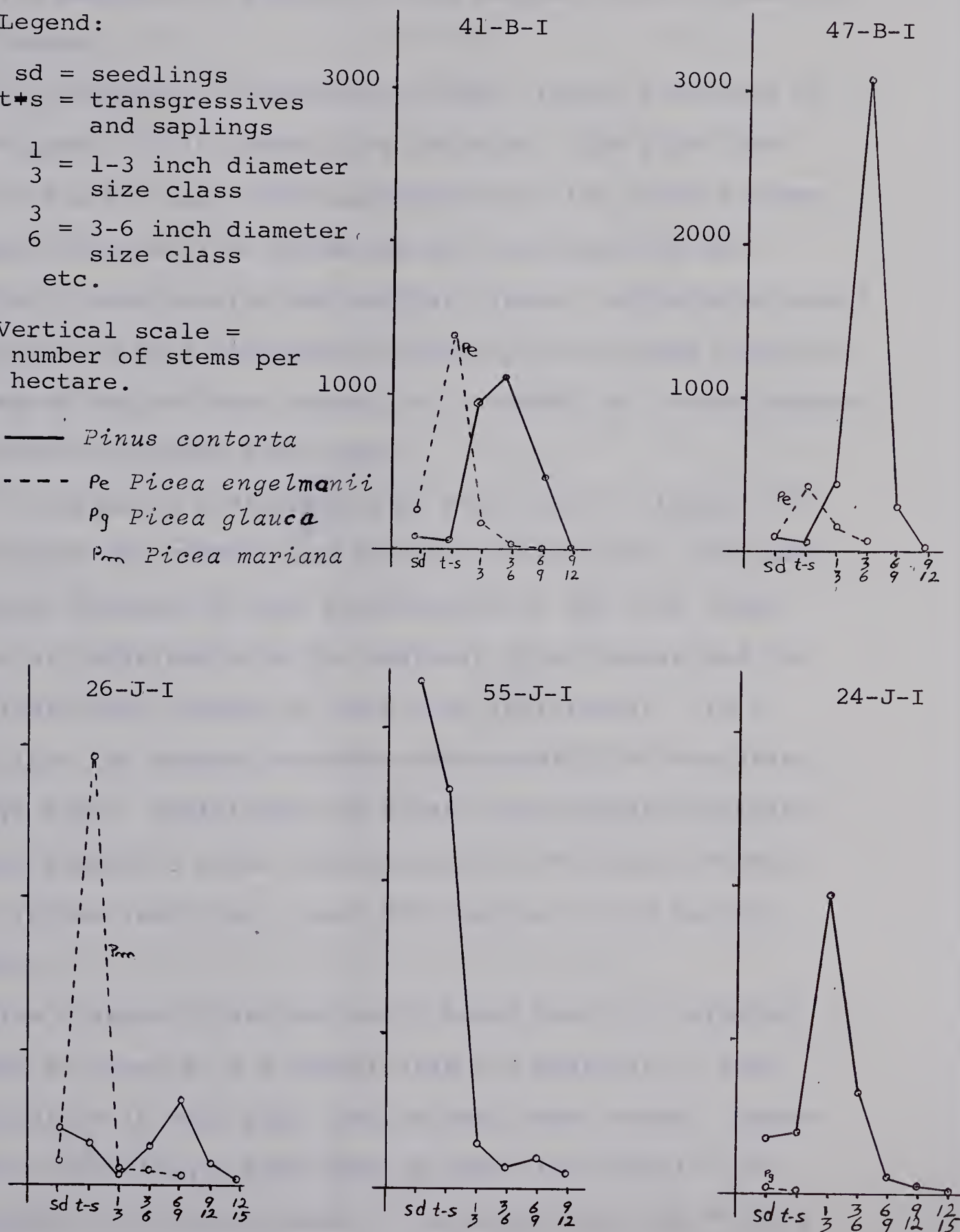
FIGURE 17. FREQUENCY DISTRIBUTIONS OF SIZE CLASSES IN INTENSIVE STANDS.

Legend:

sd = seedlings
 t+s = transgressives
 and saplings
 1 = 1-3 inch diameter
 size class
 3 = 3-6 inch diameter
 size class
 etc.

Vertical scale =
 number of stems per
 hectare.

— *Pinus contorta*
 --- *Pe Picea engelmannii*
Pg Picea glauca
Pm Picea mariana



lasiocarpa, although not shown in the Figures due to its very low numbers, is present in the smallest size classes in both stands.

The Frequency distribution of DBH classes for stand 26-J-I (Figure 17) is bimodal for the pine. The right hand peak at the 6-9 inch DBH class represents the initial regeneration following fire while the left hand peak in the seedling, transgressive and sapling classes indicates a recent resurgence in pine reproduction probably associated with the opening of the old tree canopy as it breaks up. *Picea mariana* is actively invading this stand.

The diameter distribution of stand 55-J-I (Figure 17) illustrates the overall low density of the stand. The most prominent feature of this distribution is the very large number of individuals in the smallest size classes and the relatively small number of tree-size individuals. This means that the present reproductive potential of the pine is very high. Individuals of other tree species are scarce - 9 *Picea glauca*, 9 *Abies lasiocarpa*, and 44 *Populus tremuloides* in the less than 1 inch DBH classes in the hectare sampled.

The diameter distribution of stand 24-J-I is similar to that of stand 55-J-I except that the quantity of pine reproduction is very much less in the former stand. Reproduction (less than 1 inch DBH) of other tree species is negligible - 28 *Picea glauca*, 7 *Picea mariana*, and 8 *Abies lasiocarpa* per hectare.

2. SHRUB STRATUM

Menziesia glabella, *Shepherdia canadensis* and *Juniperus communis* are the only shrubs important to the community structure of the five intensive stands. *Rosa acicularis* has high Frequency (Table 18) in the three Jasper stands but it has low cover (Table 19) and is not a conspicuous component of the shrub stratum. *Lonicera involucrata* is restricted to the two moist, high subalpine, Banff stands; it has high Frequency but low cover in stand 47-B-I. *Ledum groenlandicum* is indicative of moist habitats and therefore has higher cover and Frequency in stands 41-B-I and 47-B-I than in the other two stands in which it occurs.

Within pine forests in the two Parks, *Ledum* appears to reach its greatest population size and vitality in moist forests at high elevation although at lower elevations in moist forests of *Picea mariana* in the Parks, it is very abundant. The reason that the *Ledum* is not better developed in what I call moist, low-elevation, pine forests may be that these "moist" forests are simply not moist enough for good *Ledum* growth.

3. HERB-DWARF SHRUB AND BRYOPHYTE-LICHEN STRATA

The plants of these two strata are generally not well developed (i.e. small population or low vitality or both) in these five stands with the exception of *Vaccinium scoparium* in 47-B-I, feather mosses in 26-J-I and 47-B-I, and *Arctostaphylos uva-ursi* in 24-J-I. Aside from one or two very abundant species which dominate these strata, the

TABLE 20.

SHRUBS: HEIGHT cm

| | 41-B-I | 47-B-I | 26-J-I | 55-J-I | 24-J-I |
|------------------------------|--------|--------|--------|--------|--------|
| <i>Menziesia glabella</i> | 120 | 90 | -- | 25 | -- |
| <i>Shepherdia canadensis</i> | 100 | 105 | 75 | 110 | 75 |
| <i>Juniperus communis</i> | 25 | 30 | 50 | 45 | 50 |
| <i>Ledum groenlandicum</i> | 40 | 30 | 35 | 30 | -- |
| <i>Rosa acicularis</i> | -- | 15 | 25 | 30 | 15 |
| <i>Lonicera involucrata</i> | 30 | 35 | -- | -- | -- |

TABLE 19.

SHRUBS: PER CENT COVER (from 2500 point samples)

| | | | | | |
|------------------------------|-------|------|------|------|------|
| <i>Menziesia glabella</i> | 28.12 | 0.08 | -- | r | -- |
| <i>Shepherdia canadensis</i> | 4.00 | 2.88 | 0.92 | 7.28 | 0.64 |
| <i>Juniperus communis</i> | r | 0.04 | 0.88 | 4.56 | 0.52 |
| <i>Ledum groenlandicum</i> | 0.88 | 0.16 | r | r | -- |
| <i>Rosa acicularis</i> | -- | r | 0.76 | 1.52 | 0.96 |
| <i>Lonicera involucrata</i> | r | 0.36 | -- | -- | -- |

TABLE 18.

PER CENT FREQUENCY - TREES AND SHRUBS

| | | | | | |
|---------------------------------|----|------|----|----|------|
| <i>Pinus contorta</i> | 98 | 100 | 94 | 73 | 70 |
| <i>Picea glauca/engelmannii</i> | 29 | 44 | 1 | -- | 0.25 |
| <i>Picea mariana</i> | -- | -- | 37 | -- | 0.5 |
| <i>Populus tremuloides</i> | -- | -- | 4 | -- | -- |
| <i>Abies lasiocarpa</i> | 7 | 0.25 | -- | -- | -- |
| <i>Menziesia glabella</i> | 96 | 31 | -- | 5 | -- |
| <i>Shepherdia canadensis</i> | 71 | 66 | 88 | 99 | 80 |
| <i>Juniperus communis</i> | 10 | 29 | 23 | 90 | 35 |
| <i>Ledum groenlandicum</i> | 45 | 17 | 6 | 2 | -- |
| <i>Rosa acicularis</i> | -- | 8 | 84 | 85 | 60 |
| <i>Lonicera involucrata</i> | 10 | 86 | -- | -- | -- |

| Table 1: Summary of data for the first part of the study | | | | |
|--|------------|------------|------------|------------|
| Group | Variable 1 | Variable 2 | Variable 3 | Variable 4 |
| 1 | 10 | 20 | 30 | 40 |
| 2 | 15 | 25 | 35 | 45 |
| 3 | 20 | 30 | 40 | 50 |
| 4 | 25 | 35 | 45 | 55 |
| 5 | 30 | 40 | 50 | 60 |
| 6 | 35 | 45 | 55 | 65 |
| 7 | 40 | 50 | 60 | 70 |
| 8 | 45 | 55 | 65 | 75 |
| 9 | 50 | 60 | 70 | 80 |
| 10 | 55 | 65 | 75 | 85 |
| 11 | 60 | 70 | 80 | 90 |
| 12 | 65 | 75 | 85 | 95 |
| 13 | 70 | 80 | 90 | 100 |
| 14 | 75 | 85 | 95 | 105 |
| 15 | 80 | 90 | 100 | 110 |
| 16 | 85 | 95 | 105 | 115 |
| 17 | 90 | 100 | 110 | 120 |
| 18 | 95 | 105 | 115 | 125 |
| 19 | 100 | 110 | 120 | 130 |
| 20 | 105 | 115 | 125 | 135 |
| 21 | 110 | 120 | 130 | 140 |
| 22 | 115 | 125 | 135 | 145 |
| 23 | 120 | 130 | 140 | 150 |
| 24 | 125 | 135 | 145 | 155 |
| 25 | 130 | 140 | 150 | 160 |
| 26 | 135 | 145 | 155 | 165 |
| 27 | 140 | 150 | 160 | 170 |
| 28 | 145 | 155 | 165 | 175 |
| 29 | 150 | 160 | 170 | 180 |
| 30 | 155 | 165 | 175 | 185 |
| 31 | 160 | 170 | 180 | 190 |
| 32 | 165 | 175 | 185 | 195 |
| 33 | 170 | 180 | 190 | 200 |
| 34 | 175 | 185 | 195 | 205 |
| 35 | 180 | 190 | 200 | 210 |
| 36 | 185 | 195 | 205 | 215 |
| 37 | 190 | 200 | 210 | 220 |
| 38 | 195 | 205 | 215 | 225 |
| 39 | 200 | 210 | 220 | 230 |
| 40 | 205 | 215 | 225 | 235 |
| 41 | 210 | 220 | 230 | 240 |
| 42 | 215 | 225 | 235 | 245 |
| 43 | 220 | 230 | 240 | 250 |
| 44 | 225 | 235 | 245 | 255 |
| 45 | 230 | 240 | 250 | 260 |
| 46 | 235 | 245 | 255 | 265 |
| 47 | 240 | 250 | 260 | 270 |
| 48 | 245 | 255 | 265 | 275 |
| 49 | 250 | 260 | 270 | 280 |
| 50 | 255 | 265 | 275 | 285 |
| 51 | 260 | 270 | 280 | 290 |
| 52 | 265 | 275 | 285 | 295 |
| 53 | 270 | 280 | 290 | 300 |
| 54 | 275 | 285 | 295 | 305 |
| 55 | 280 | 290 | 300 | 310 |
| 56 | 285 | 295 | 305 | 315 |
| 57 | 290 | 300 | 310 | 320 |
| 58 | 295 | 305 | 315 | 325 |
| 59 | 300 | 310 | 320 | 330 |
| 60 | 305 | 315 | 325 | 335 |
| 61 | 310 | 320 | 330 | 340 |
| 62 | 315 | 325 | 335 | 345 |
| 63 | 320 | 330 | 340 | 350 |
| 64 | 325 | 335 | 345 | 355 |
| 65 | 330 | 340 | 350 | 360 |
| 66 | 335 | 345 | 355 | 365 |
| 67 | 340 | 350 | 360 | 370 |
| 68 | 345 | 355 | 365 | 375 |
| 69 | 350 | 360 | 370 | 380 |
| 70 | 355 | 365 | 375 | 385 |
| 71 | 360 | 370 | 380 | 390 |
| 72 | 365 | 375 | 385 | 395 |
| 73 | 370 | 380 | 390 | 400 |
| 74 | 375 | 385 | 395 | 405 |
| 75 | 380 | 390 | 400 | 410 |
| 76 | 385 | 395 | 405 | 415 |
| 77 | 390 | 400 | 410 | 420 |
| 78 | 395 | 405 | 415 | 425 |
| 79 | 400 | 410 | 420 | 430 |
| 80 | 405 | 415 | 425 | 435 |
| 81 | 410 | 420 | 430 | 440 |
| 82 | 415 | 425 | 435 | 445 |
| 83 | 420 | 430 | 440 | 450 |
| 84 | 425 | 435 | 445 | 455 |
| 85 | 430 | 440 | 450 | 460 |
| 86 | 435 | 445 | 455 | 465 |
| 87 | 440 | 450 | 460 | 470 |
| 88 | 445 | 455 | 465 | 475 |
| 89 | 450 | 460 | 470 | 480 |
| 90 | 455 | 465 | 475 | 485 |
| 91 | 460 | 470 | 480 | 490 |
| 92 | 465 | 475 | 485 | 495 |
| 93 | 470 | 480 | 490 | 500 |
| 94 | 475 | 485 | 495 | 505 |
| 95 | 480 | 490 | 500 | 510 |
| 96 | 485 | 495 | 505 | 515 |
| 97 | 490 | 500 | 510 | 520 |
| 98 | 495 | 505 | 515 | 525 |
| 99 | 500 | 510 | 520 | 530 |
| 100 | 505 | 515 | 525 | 535 |
| 101 | 510 | 520 | 530 | 540 |
| 102 | 515 | 525 | 535 | 545 |
| 103 | 520 | 530 | 540 | 550 |
| 104 | 525 | 535 | 545 | 555 |
| 105 | 530 | 540 | 550 | 560 |
| 106 | 535 | 545 | 555 | 565 |
| 107 | 540 | 550 | 560 | 570 |
| 108 | 545 | 555 | 565 | 575 |
| 109 | 550 | 560 | 570 | 580 |
| 110 | 555 | 565 | 575 | 585 |
| 111 | 560 | 570 | 580 | 590 |
| 112 | 565 | 575 | 585 | 595 |
| 113 | 570 | 580 | 590 | 600 |
| 114 | 575 | 585 | 595 | 605 |
| 115 | 580 | 590 | 600 | 610 |
| 116 | 585 | 595 | 605 | 615 |
| 117 | 590 | 600 | 610 | 620 |
| 118 | 595 | 605 | 615 | 625 |
| 119 | 600 | 610 | 620 | 630 |
| 120 | 605 | 615 | 625 | 635 |
| 121 | 610 | 620 | 630 | 640 |
| 122 | 615 | 625 | 635 | 645 |
| 123 | 620 | 630 | 640 | 650 |
| 124 | 625 | 635 | 645 | 655 |
| 125 | 630 | 640 | 650 | 660 |
| 126 | 635 | 645 | 655 | 665 |
| 127 | 640 | 650 | 660 | 670 |
| 128 | 645 | 655 | 665 | 675 |
| 129 | 650 | 660 | 670 | 680 |
| 130 | 655 | 665 | 675 | 685 |
| 131 | 660 | 670 | 680 | 690 |
| 132 | 665 | 675 | 685 | 695 |
| 133 | 670 | 680 | 690 | 700 |
| 134 | 675 | 685 | 695 | 705 |
| 135 | 680 | 690 | 700 | 710 |
| 136 | 685 | 695 | 705 | 715 |
| 137 | 690 | 700 | 710 | 720 |
| 138 | 695 | 705 | 715 | 725 |
| 139 | 700 | 710 | 720 | 730 |
| 140 | 705 | 715 | 725 | 735 |
| 141 | 710 | 720 | 730 | 740 |
| 142 | 715 | 725 | 735 | 745 |
| 143 | 720 | 730 | 740 | 750 |
| 144 | 725 | 735 | 745 | 755 |
| 145 | 730 | 740 | 750 | 760 |
| 146 | 735 | 745 | 755 | 765 |
| 147 | 740 | 750 | 760 | 770 |
| 148 | 745 | 755 | 765 | 775 |
| 149 | 750 | 760 | 770 | 780 |
| 150 | 755 | 765 | 775 | 785 |
| 151 | 760 | 770 | 780 | 790 |
| 152 | 765 | 775 | 785 | 795 |
| 153 | 770 | 780 | 790 | 800 |
| 154 | 775 | 785 | 795 | 805 |
| 155 | 780 | 790 | 800 | 810 |
| 156 | 785 | 795 | 805 | 815 |
| 157 | 790 | 800 | 810 | 820 |
| 158 | 795 | 805 | 815 | 825 |
| 159 | 800 | 810 | 820 | 830 |
| 160 | 805 | 815 | 825 | 835 |
| 161 | 810 | 820 | 830 | 840 |
| 162 | 815 | 825 | 835 | 845 |
| 163 | 820 | 830 | 840 | 850 |
| 164 | 825 | 835 | 845 | 855 |
| 165 | 830 | 840 | 850 | 860 |
| 166 | 835 | 845 | 855 | 865 |
| 167 | 840 | 850 | 860 | 870 |
| 168 | 845 | 855 | 865 | 875 |
| 169 | 850 | 860 | 870 | 880 |
| 170 | 855 | 865 | 875 | 885 |
| 171 | 860 | 870 | 880 | 890 |
| 172 | 865 | 875 | 885 | 895 |
| 173 | 870 | 880 | 890 | 900 |
| 174 | 875 | 885 | 895 | 905 |
| 175 | 880 | 890 | 900 | 910 |
| 176 | 885 | 895 | 905 | 915 |
| 177 | 890 | 900 | 910 | 920 |
| 178 | 895 | 905 | 915 | 925 |
| 179 | 900 | 910 | 920 | 930 |
| 180 | 905 | 915 | 925 | 935 |
| 181 | 910 | 920 | 930 | 940 |
| 182 | 915 | 925 | 935 | 945 |
| 183 | 920 | 930 | 940 | 950 |
| 184 | 925 | 935 | 945 | 955 |
| 185 | 930 | 940 | 950 | 960 |
| 186 | 935 | 945 | 955 | 965 |
| 187 | 940 | 950 | 960 | 970 |
| 188 | 945 | 955 | 965 | 975 |
| 189 | 950 | 960 | 970 | 980 |
| 190 | 955 | 965 | 975 | 985 |
| 191 | 960 | 970 | 980 | 990 |
| 192 | 965 | 975 | 985 | 995 |
| 193 | 970 | 980 | 990 | 1000 |
| 194 | 975 | 985 | 995 | 1005 |
| 195 | 980 | 990 | 1000 | 1010 |
| 196 | 985 | 995 | 1005 | 1015 |
| 197 | 990 | 1000 | 1010 | 1020 |
| 198 | 995 | 1005 | 1015 | 1025 |
| 199 | 1000 | 1010 | 1020 | 1030 |
| 200 | 1005 | 1015 | 1025 | 1035 |
| 201 | 1010 | 1020 | 1030 | 1040 |
| 202 | 1015 | 1025 | 1035 | 1045 |
| 203 | 1020 | 1030 | 1040 | 1050 |
| 204 | 1025 | 1035 | 1045 | 1055 |
| 205 | 1030 | 1040 | 1050 | 1060 |
| 206 | 1035 | 1045 | 1055 | 1065 |
| 207 | 1040 | 1050 | 1060 | 1070 |
| 208 | 1045 | 1055 | 1065 | 1075 |
| 209 | 1050 | 1060 | 1070 | 1080 |
| 210 | 1055 | 1065 | 1075 | 1085 |
| 211 | 1060 | 1070 | 1080 | 1090 |
| 212 | 1065 | 1075 | 1085 | 1095 |
| 213 | 1070 | 1080 | 1090 | 1100 |
| 214 | 1075 | 1085 | 1095 | 1105 |
| 215 | 1080 | 1090 | 1100 | 1110 |
| 216 | 1085 | 1095 | 1105 | 1115 |
| 217 | 1090 | 1100 | 1110 | 1120 |
| 218 | 1095 | 1105 | 1115 | 1125 |
| 219 | 1100 | 1110 | 1120 | 1130 |
| 220 | 1105 | 1115 | 1125 | 1135 |
| 221 | 1110 | 1120 | 1130 | 1140 |
| 222 | 1115 | 1125 | 1135 | 1145 |
| 223 | 1120 | 1130 | 1140 | 1150 |
| 224 | 1125 | 1135 | 1145 | 1155 |
| 225 | 1130 | 1140 | 1150 | 1160 |
| 226 | 1135 | 1145 | 1155 | 1165 |
| 227 | 1140 | 1150 | 1160 | 1170 |
| 228 | 1145 | 1155 | 1165 | 1175 |
| 229 | 1150 | 1160 | 1170 | 1180 |
| 230 | 1155 | 1165 | 1175 | 1185 |
| 231 | 1160 | 1170 | 1180 | 1190 |
| 232 | 1165 | 1175 | 1185 | 1195 |
| 233 | 1170 | 1180 | 1190 | 1200 |
| 234 | 1175 | 1185 | 1195 | 1205 |
| 235 | 1180 | 1190 | 1200 | 1210 |
| 236 | 1185 | 1195 | 1205 | 1215 |
| 237 | 1190 | 1200 | 1210 | 1220 |
| 238 | 1195 | 1205 | 1215 | 1225 |
| 239 | 1200 | 1210 | 1220 | 1230 |
| 240 | 1205 | 1215 | 1225 | 1235 |
| 241 | 1210 | 1220 | 1230 | 1240 |
| 242 | 1215 | 1225 | 1235 | 1245 |
| 243 | 1220 | 1230 | 1240 | 1250 |
| 244 | 1225 | 1235 | 1245 | 1255 |
| 245 | 1230 | 1240 | 1250 | 1260 |
| 246 | 1235 | 1245 | 1255 | 1265 |
| 247 | 1240 | 1250 | 1260 | 1270 |
| 248 | 1245 | 1255 | 1265 | 1275 |
| 249 | 1250 | 1260 | 1270 | 1280 |
| 250 | 1255 | 1265 | 1275 | 1285 |
| 251 | 1260 | 1270 | 1280 | 1290 |
| 252 | 1265 | 1275 | 1285 | 1295 |
| 253 | 1270 | 1280 | 1290 | 1300 |
| 254 | 1275 | 1285 | 1295 | 1305 |
| 255 | 1280 | 1290 | 1300 | 1310 |
| 256 | 1285 | 1295 | 1305 | 1315 |
| 257 | 1290 | 1300 | 1310 | 1320 |
| 258 | 1295 | 1305 | 1315 | 1325 |
| 259 | 1300 | 1310 | 1320 | 1330 |
| 260 | 1305 | 1315 | 1325 | 1335 |
| 261 | 1310 | 1320 | 1330 | 1340 |
| 262 | 1315 | 1325 | 1335 | 1345 |
| 263 | 1320 | 1330 | 1340 | 1350 |
| 264 | 1325 | 1335 | 1345 | 135 |

remainder of the species have low cover and either high or low Frequency. Examples of species with low cover but high Frequency are *Melampyrum lineare* and *Elymus innovatus*. A comparison of the five sites including information regarding these two lowest strata is given in the following section. A presence list of bryophytes and lichens is given in Appendix 5.

D. VEGETATIONAL COMPARISON AND CONTRAST OF INTENSIVE STANDS

This section compares the five examples of the forest types on the basis of species abundance and distribution in each of the five intensive stands. Prominence Values (after Beals 1960 and modified by La Roi 1964) for each species were the product of average percent cover in 25 quadrats and the square root of per cent Frequency in these quadrats.

From Table 12 it can be seen that some species are restricted to one or another of the five stands. This does not necessarily imply that the species are restricted to the noda of which their stands are examples. The Primary Survey has shown that many of these species are present in other forest types but usually in lesser quantities. For example, *Vaccinium vitis-idaea*, shown in Table 12 as occurring only in stand 55-J-I (the *Shepherdia* type) was also found to occur in some Feather Moss Forest stands. Similarly, *Lonicera involucrata* has been found in Feather Moss type forests and *Vaccinium myrtillus* in *Shepherdia* type forests.

Stand 41-B-I (Table 12) is clearly distinguished from the other 4 stands by the presence and abundance of:

Abies lasiocarpa (shrubs)

Menziesia glabella

Cetraria spp.

Vaccinium myrtillus

Ledum groenlandicum

The *Ledum*, *Abies*, *Menziesia*, and *Vaccinium* indicate the moistness of the habitat and the latter three of these species plus *Picea engelmannii* indicate the high elevation habitat of the stand. The abundance of *Cetraria* spp. is indicative of the frequency in this forest of openings where mineral soil is exposed. Since the tree and shrub strata both have high cover, the openings indicated by the *Cetraria* show that the individuals of the two highest strata are very contagiously distributed. The vegetational similarities between stands 41-B-I and 47-B-I are represented by *Picea engelmannii*, *Pleurozium schreberi*, and *Vaccinium scoparium*.

The species which typify (again by presence and abundance) stand 47-B-I in Table 12 are:

Arnica cordifolia

Lonicera involucrata

Aster ciliolatus

Vaccinium scoparium

Aster conspicuus

These five species are not restricted to the *Vaccinium* type nodum of which this stand is a member, but they do signify by their lush growth (a characteristic not included in Table 12) that this stand is a member of the Moist Forest class. The abundance of *Pleurozium schreberi*, and to a lesser degree *Cornus canadensis*, shows the similarity of this stand to stand 26-J-I. The *Cladonia* spp. which are abundant are primarily restricted to microhabitats of mineral

TABLE 12. PROMINENCE INDEX (max. 1000)

FOR SELECTED SPECIES FROM THE INTENSIVE STANDS

(IV = % cover x $\sqrt{\%$ Frequency; cover from 2500 cover points, Frequency from 25 intensive quadrats per stand)

| Species | Stand | 41-B-I | 47-B-I | 26-J-I | 55-J-I | 24-J-I |
|-----------------------------------|-------|--------|--------|--------|--------|--------|
| <i>Pinus contorta</i> (trees) | | 540 | 450 | 400 | 161 | 390 |
| Needles (coniferous) | | 520 | 820 | 215 | 800 | 550 |
| Moss | | 150 | 78 | 48 | 160 | 186 |
| Lichens | | 9.6 | 6.0 | 19.0 | 6.3 | 36.6 |
| <i>Peltigera</i> spp. | | 57.5 | 26.2 | 107.8 | 137.2 | 80.0 |
| <i>Linnaea borealis</i> | | 18.0 | 39.2 | 98.0 | 137.2 | 36.1 |
| <i>Shepherdia canadensis</i> | | 29.9 | 19.0 | 7.5 | 67.1 | 4.5 |
| Liverworts | | 65.7 | 7.2 | 55.0 | 71.6 | 1.5 |
| <i>Achillea millefolium</i> | | -- | -- | -- | 0.1 | 2.3 |
| <i>Fragaria virginiana</i> | | -- | 0.1 | 0.1 | 17.0 | 17.0 |
| <i>Elymus innovatus</i> | | -- | 39.2 | 50.0 | 14.0 | 68.6 |
| <i>Arctostaphylos uva-ursi</i> | | -- | -- | 20.8 | 38.4 | 290.0 |
| <i>Rosa acicularis</i> | | -- | -- | 6.0 | 14.4 | 7.5 |
| <i>Juniperus communis</i> | | -- | 0.1 | 5.7 | 38.7 | 3.5 |
| <i>Vaccinium caespitosum</i> | | -- | -- | 17.0 | 75.0 | -- |
| <i>Vaccinium vitis-idaea</i> | | -- | -- | -- | 0.2 | -- |
| <i>Melampyrum lineare</i> | | -- | -- | -- | 64.2 | -- |
| <i>Picea mariana</i> (tree) | | -- | -- | 39.8 | -- | 0.2 |
| <i>Populus tremuloides</i> (tree) | | -- | 0.02 | 4.0 | -- | 0.3 |
| <i>Cladonia</i> spp. | | -- | 137.2 | -- | 196.0 | -- |
| <i>Dicranum polysetum</i> | | 8.0 | 7.2 | 58.8 | 8.0 | -- |
| <i>Polytrichum juniperinum</i> | | 0.8 | 1.6 | 2.0 | 6.9 | -- |
| <i>Picea engelmannii</i> (tree) | | 16.5 | 19.9 | -- | -- | -- |
| <i>Ptilium crista-castrensis</i> | | 6.0 | 27.5 | 4.9 | 24.0 | -- |
| <i>Pleurozium schreberi</i> | | 178.2 | 450.0 | 290.0 | 225.0 | -- |
| <i>Hylocomium splendens</i> | | 0.3 | 2.3 | 280.0 | 0.8 | -- |
| <i>Cornus canadensis</i> | | 0.3 | 58.8 | 22.4 | 0.1 | -- |
| <i>Arnica cordifolia</i> | | 7.2 | 58.8 | 1.2 | 0.2 | -- |
| <i>Aster ciliolatus</i> | | -- | 8.0 | -- | 0.1 | -- |
| <i>Vaccinium scoparium</i> | | 70.0 | 290.0 | -- | 0.2 | -- |
| <i>Aster conspicuus</i> | | -- | 2.4 | 0.2 | 0.1 | -- |
| <i>Lonicera involucrata</i> | | -- | 2.0 | -- | -- | -- |
| <i>Abies lasiocarpa</i> (shrub) | | 9.8 | -- | -- | 0.2 | -- |
| <i>Ledum groenlandicum</i> | | 4.9 | 0.6 | -- | -- | -- |
| <i>Menziesia glabella</i> | | 262.7 | 0.3 | -- | -- | -- |
| <i>Vaccinium myrtillus</i> | | 2.7 | -- | -- | -- | -- |
| <i>Cetraria</i> spp. | | 100.0 | -- | -- | 7.5 | -- |

"Boxed" values indicate the stands in which the species have character value.

soil and very rotten wood. The abundance of *Cladonia* spp. in both stands 47-B-I and 55-J-I does not show habitat similarities, because the variety, form, and often the species of *Cladonia* were different between the two sites and these taxonomic differences appear to correlate with habitat differences.

Stand 26-J-I is distinguished in Table 12 from the other four stands by the following species:

Dicranum polysetum

Picea mariana

Hylocomium splendens

Populus tremuloides

Picea mariana is indicative of moist sites and itself may create or maintain a moist and shaded habitat in which *Hylocomium* flourishes. The abundance of *Dicranum polysetum* signifies an abundance of rotting wood in a cool moist forest. Besides being related to stand 47-B-I as described above (see also Table 12), stand 26-J-I is also related to stand 55-J-I which is a mesophytic type of forest. The abundance of *Pleurozium schreberi*, *Linnaea borealis* and *Peltigera* spp. show the ecological similarities of these latter two stands.

Stand 55-J-I has the following species which in Table 12 appear to characterize this stand:

Juniperus communis

Shepherdia canadensis

Melampyrum lineare

Vaccinium caespitosum

Rosa acicularis

Vaccinium vitis-idaea

By comparing this list of species with those given above for the previous three stands, it can be seen that the species

typifying stand 55-J-I are species of mesic to dry habitats as compared with the moist habitats of the other three stands. The abundance of *Cladonia* spp. such as *C. pyxidata* and *Peltigera* spp. such as *P. canina* shows that this stand is open and tending towards the dry-mesophytic type of forest.

In addition to the moist stand relationships described above, stand 55-J-I is related to the xerophytic stand 24-J-I by the abundance of *Fragaria virginiana*. Because nearly all species in stand 24-J-I have low abundance, there are species other than *Fragaria* which indicate ecological affinities between 55-J-I and 24-J-I although the species have much lower abundance in the latter stand. Such species are:

Juniperus communis

Peltigera canina

Linnaea borealis

Rosa acicularis

Achillea millefolium, *Arctostaphylos uva-ursi* and *Elymus innovatus* are the only species in Table 12, which really distinguish stand 24-J-I from the rest of the stands. This is understandable considering the sparseness of the vegetation in this stand. These three species indicate a strong floristic affinity to stand 26-J-I.

The species listed below do not appear in Table 12 primarily because of their small population sizes but they do have character value (*sensu* Braun-Blanquet 1932) in the intensive stands.

41-B-I: *Lycopodium annotinum*

Phyllodoce spp.

| | |
|---------|--------------------------------|
| | <i>Rhododendron albiflorum</i> |
| 55-J-I: | <i>Gentianella amarella</i> |
| | <i>Solidago decumbens</i> |
| | <i>Solidago multiradiata</i> |
| 24-J-I: | <i>Amelanchier alnifolia</i> |
| | <i>Festuca saximontana</i> |
| | <i>Gentianella amarella</i> |
| | <i>Senecio cymbalarioides</i> |
| | <i>Solidago decumbens.</i> |

An index of similarity (see p. 33) was calculated for the five Intensive Stands (Table 13). From the sums of the indices of similarity for each it can be seen that stand 24-J-I bears the least resemblance to the other four stands, and stand 55-J-I bears the most. The lack of similarity between 24-J-I and the other stands emphasizes how vegetationally different the xerophytic stand is when compared with the mesophytic and moist stands. The high species diversity and intermediate habitat of stand 55-J-I in part accounts for its over-all high similarity to the other four stands. A common, fairly high abundance of *Pleurozium schreberi* in the four moist and mesophytic stands accounts in part for the high similarity (relative to that with 24-J-I) between the four stands. However, on an absolute basis, the similarities between the five stands must be considered low (the index can range from 0.0 to 1.0). The low values may be accounted for by: (1) the small number of species in common between each type, and (2) the very

prominent quantitative differences in the species present in each of the stands.

TABLE 13. INDICES OF SIMILARITY BETWEEN THE FIVE INTENSIVE STANDS based upon the Prominence Indices in Table 12 excluding the values for *Pinus contorta* (trees) and needles (coniferous)

| | 41-B-I | 47-B-I | 26-J-I | 55-J-I | 24-J-I | Totals of each stand |
|--------|--------|--------|--------|--------|--------|-------------------------|
| 41-B-I | -- | | | | | 1.50 |
| 47-B-I | .39 | -- | | | | 1.41 |
| 26-J-I | .36 | .43 | -- | | | 1.59 |
| 55-J-I | .46 | .45 | .51 | -- | | 1.78 |
| 24-J-I | .29 | .14 | .29 | .36 | -- | 1.08 |

E. POPULATION-PATTERNS AND SUCCESSIONAL STATUS

1. STAND 41-B-I : TREE STRATUM

The northwest corner of stand 41-B-I crosses a fire margin. The trees in the older area are variable in age - from 139 years for an *Abies lasiocarpa* to 261 years for a *Pinus contorta* and 276 years for a *Picea engelmannii*. A core taken from a standing dead pine tree of a previous forest in the younger area yielded an age of 174 years; a living pine at the edge of the most recent fire margin was found to be 165 years old. Most of the present stand is about 87 years old. It would appear then that a fire occurred in the area about 180 years ago then again about

90 years ago. In both instances the area north of the plot escaped the fire or was only burned by a small ground fire. The trees in the older area have served as a source of seed for the present stand and probably for the stand immediately prior to this one.

Regeneration of the pine forest has taken at least 20 - 30 years, as appears to be the case with many of the pine forests in the two Parks. The distribution of ages across the plot (Figure 21) shows the youngest trees furthest from the fire margin in the northwest. There is another tree seed-source approximately 20 - 40 m below the west end of the plot. Here, several large trees growing in a wet depression escaped the last fire. This additional, relatively close source of seed complicates the gradients of ages which would be expected if the primary source of seed had been only from the northwest.

Running counter to the tendency for younger ages at greater distances from the fire margin, is the tendency for pine density to be greater at increasing distances from the northeast fire margin (Figure 22). It is possible that the initial seeding of pine immediately following the fire did not yield a fully stocked forest such that regeneration continued for 20 - 30 years. During this period, *Picea* as well as *Pinus* were seeding in the area. From Figure 23 it is clear that the *Picea* are invading the area much more slowly than the pine but the former are reproducing in large numbers (see Figure 25). *Picea* density is high

FIGURE 21

41-B-I

Pinus contorta

age/ DBH (inches)

| | | | | |
|--------|--------|--------|--------|--------|
| 77/2.1 | | | | |
| | | | 90/7.0 | |
| | | 68/3.6 | | |
| 57/3.4 | | | | 86/8.7 |
| | | 84/3.7 | 76/4.2 | |
| | | 86/6.7 | | 77/5.0 |
| 85/5.6 | | | | |
| 85/5.1 | | | 79/3.0 | |
| | 84/6.0 | | | |
| | | | 69/4.0 | 49/1.8 |
| | | | 88/5.8 | 87/8.8 |
| | | 84/3.7 | | |
| | | | 85/5.7 | |
| | 89/6.7 | | | 84/6.7 |
| 80/5.4 | | | 85/6.4 | |
| | | 85/7.7 | | 86/7.8 |
| | | | | 174/14 |

FIGURE 22

41-B-I

Pinus contorta

trees

- 1= 1-3 individuals
 2= 4-5 individuals
 3= 6-8 individuals
 4= 9-15 individuals
 5= more than 15
 individuals

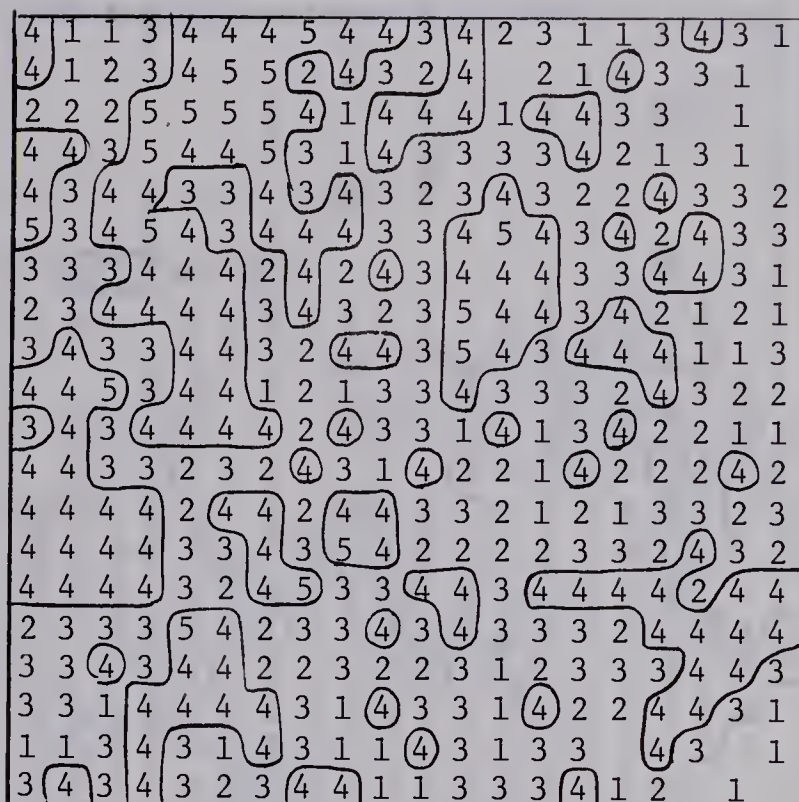


FIGURE 23

41-B-I

Picea engelmannii

trees

- 1= 1 individual
 2= 2-3 individuals
 3= 4-6 individuals

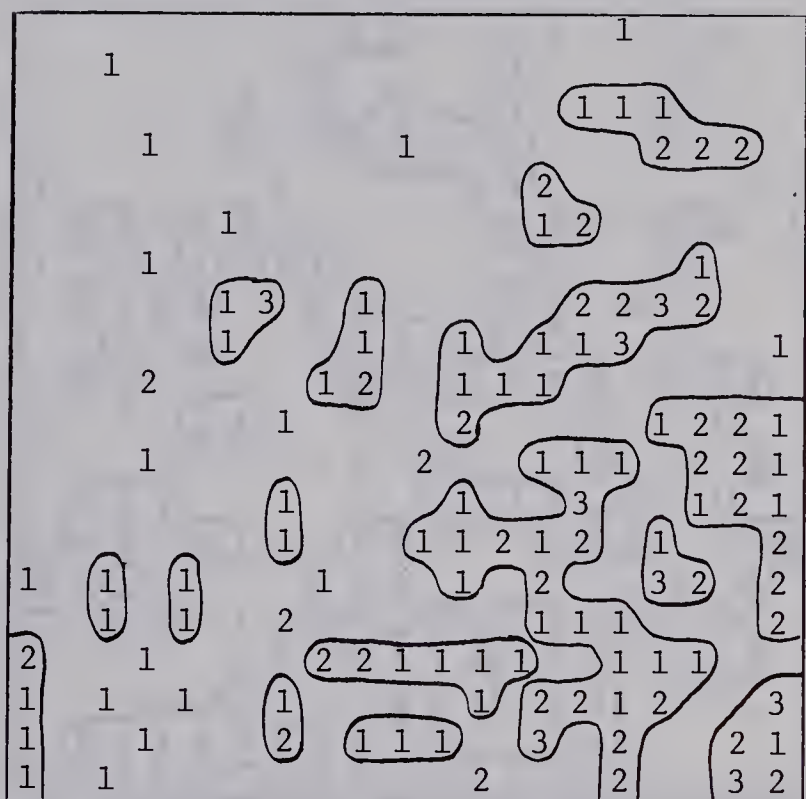


FIGURE 24

41-B-I

Pinus contorta

seedlings

numbers = actual
 numbers of individuals.

For these and subsequent
 distribution maps, see
 Table 1 for explanation
 of cover scale.

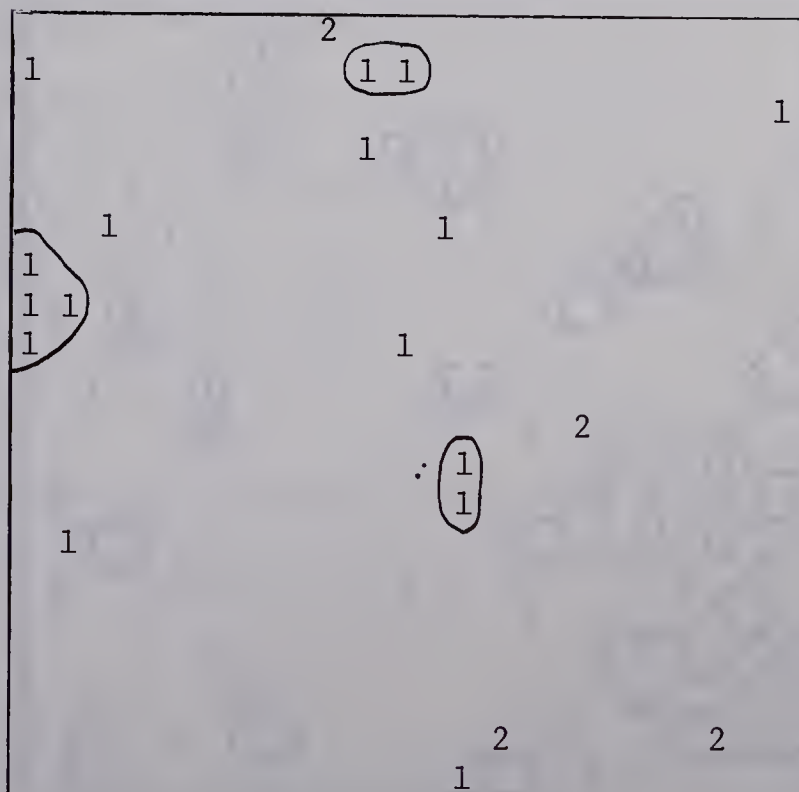


FIGURE 25

41-B-I

Picea engelmannii

transgressives

- 1= 1-3 individuals
 2= 4-6 individuals
 3= 7-19 individuals
 4= more than 19
 individuals.

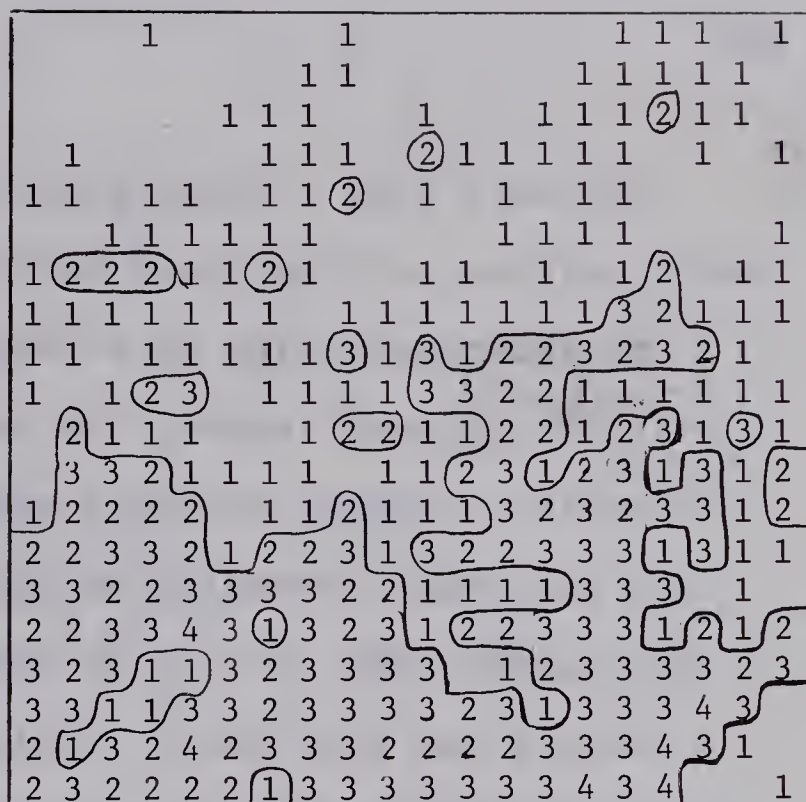


FIGURE 26

41-B-I

Picea engelmannii

seedlings

- 1= 1-3 individuals
 2= more than 3
 individuals.

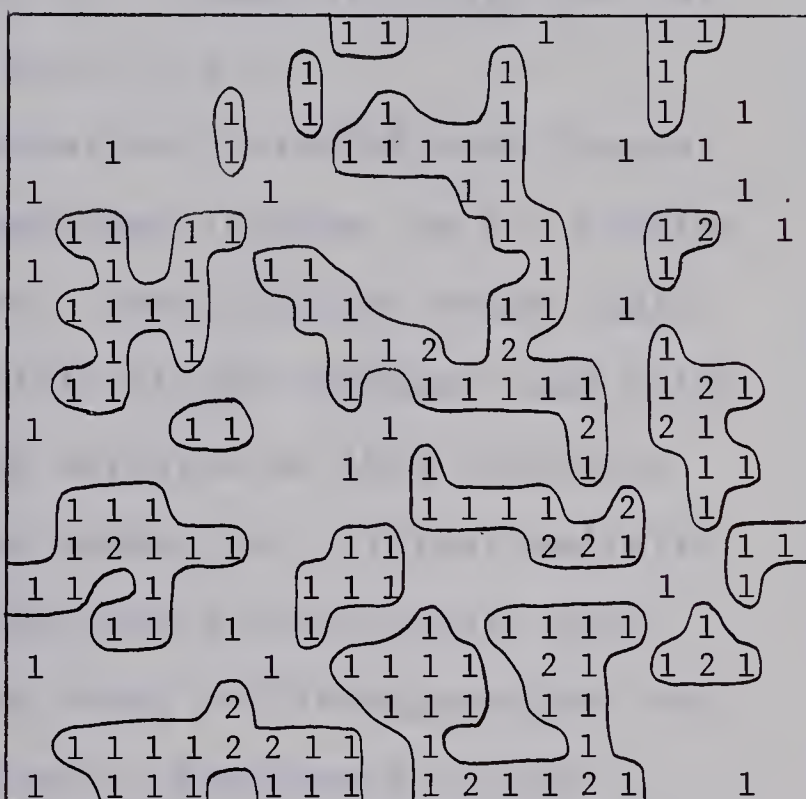


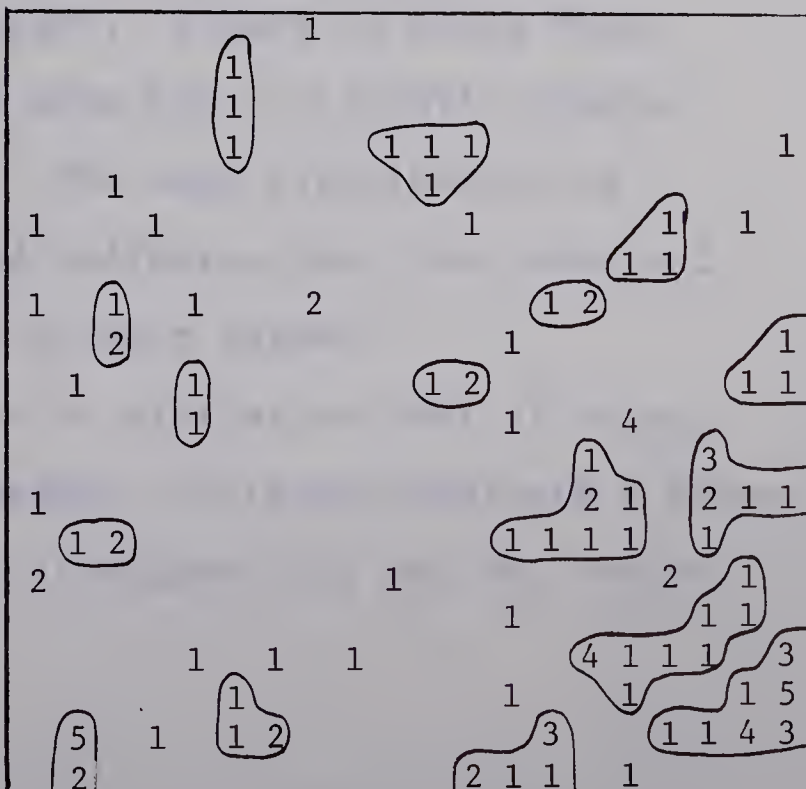
FIGURE 27

41-B-I

Abies lasiocarpa

seedlings

numbers = actual numbers
 of individuals.



near the fire margin and decreases rapidly away from it. With the more intense competition near the fire margin, sites at greater distances would tend to be more favourable to later pine regeneration. Thus the greater density of pine would be expected at sites away from the margin. Further support for this hypothesis may be gained by comparing the density of stand 41-B with that of 41-B-I. The former was located just south of the latter. Stand 41-B has a pine density of 33 while 41-B-I has 28. Stand 41-B also has far less *Picea* reproduction than does 41-B-I.

Compared to the other intensively studied pine forests, this one has very few pine seedlings (Figure 24). Precise reasons for this are not known. Possibilities which could be investigated are the viability of the abundant seed which was found; or reduced seedling survival at this elevation and/or under a dense *Menziesia* canopy; or critical deficits in available soil water at some period of the year, etc..

The distribution of *Picea* trees and transgressives has already been discussed. Of further importance is the distribution of *Picea* "seedlings". Figure 26 shows them to be abundant throughout the area but of slightly greater density near the fire margin. The wide distribution of *Picea* "seedlings" in the stand indicates that the potential for *Picea* reproduction exists in most places.

The distribution of *Abies* is similar to that of *Picea* except that *Abies* is less abundant. This may indicate a slower rate of spread of the *Abies*. If Figures 27, 28, 29, and 30

FIGURE 28

41-B-I

Abies lasiocarpa

transgressives

1= 1-5 individuals

2= more than 5 individuals

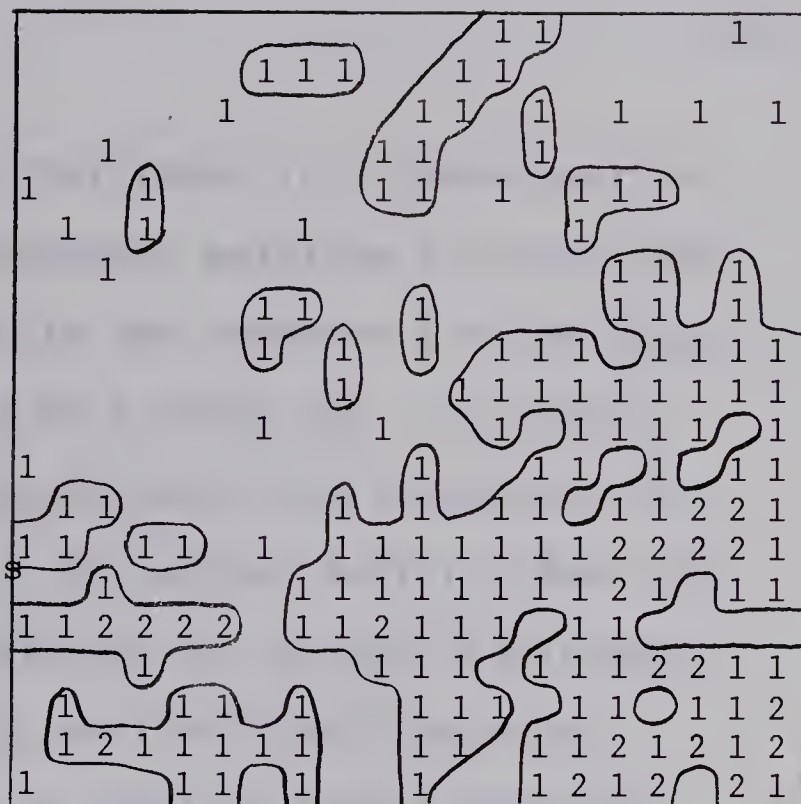


FIGURE 29

41-B-I

Abies lasiocarpa

saplings

1= 1-3 individuals

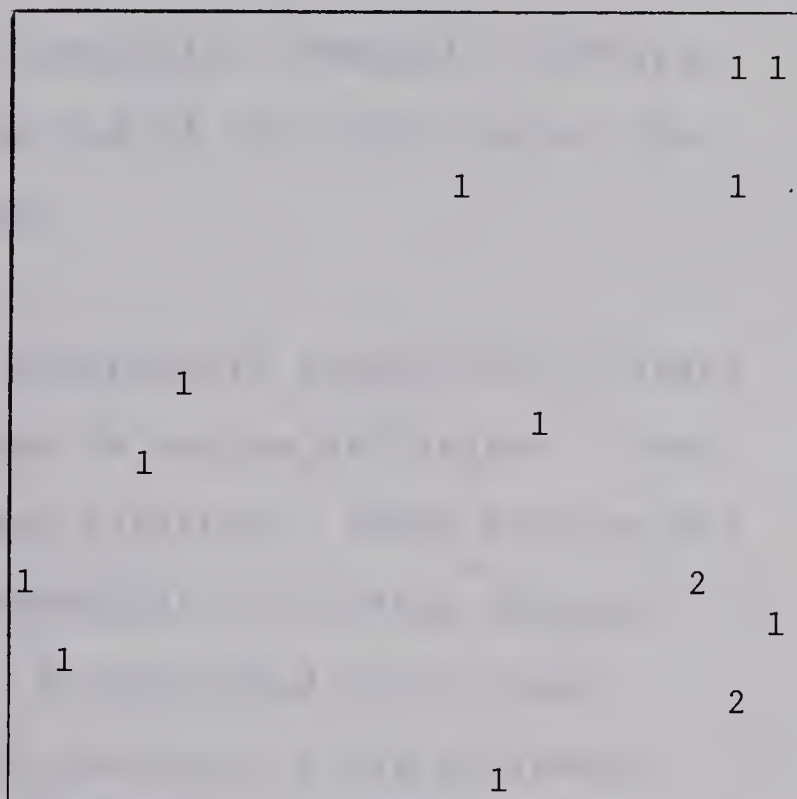
2= more than 3
individuals.

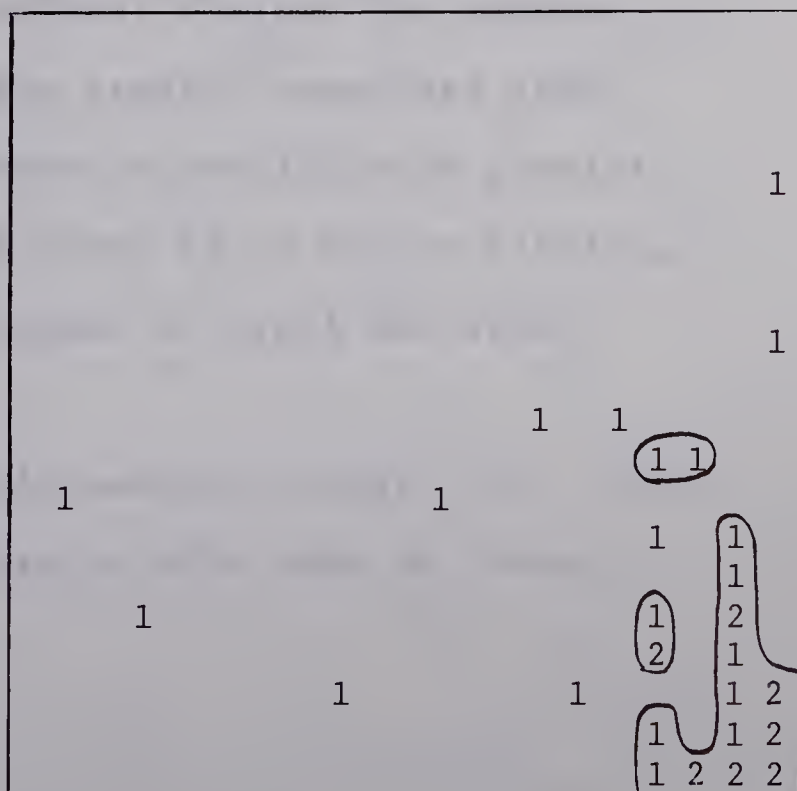
FIGURE 30

41-B-I

Abies lasiocarpa

trees

1= 1-2 individuals

2= more than 2
individuals.

are compared, it can be seen that there is a disproportionately large number of transgressives relative to other size classes; this is attributable to the tendency for the *Abies* to reproduce by layering even at a young age. In a few instances the layering appears to have been stimulated by browsing - probably by moose - but animal activity does not adequately account for the majority of layered individuals.

From the foregoing, it is obvious that this pine forest of the *Menziesia* type is seral in nature and will be succeeded by a *Picea-Abies* dominated community (barring the occurrence of fire) by the end of the life span of the present mature pine population.

THE SUBORDINATE STRATA

The distribution of the subordinate vegetation in stand 41-B-I appears to be controlled by two major factors - tree density (particularly *Picea*) and moisture. These factors are themselves related and interdependent to varying degrees throughout the studied area. As described above, *Picea* density of all size-classes is greatest in the northwest and decreases towards the southeast whereas the reverse is true for *Pinus*. Because of the greater cover and shade produced by the *Picea*, its presence should be of greater significance than that of the *Pinus* in so far as limiting the distribution of plants because of light and water interception.

The distribution of *Pyrola secunda* (Figure 32) has the strongest negative correlation with that of *Picea*.

FIGURE 31

Cornus canadensis

41-B-I

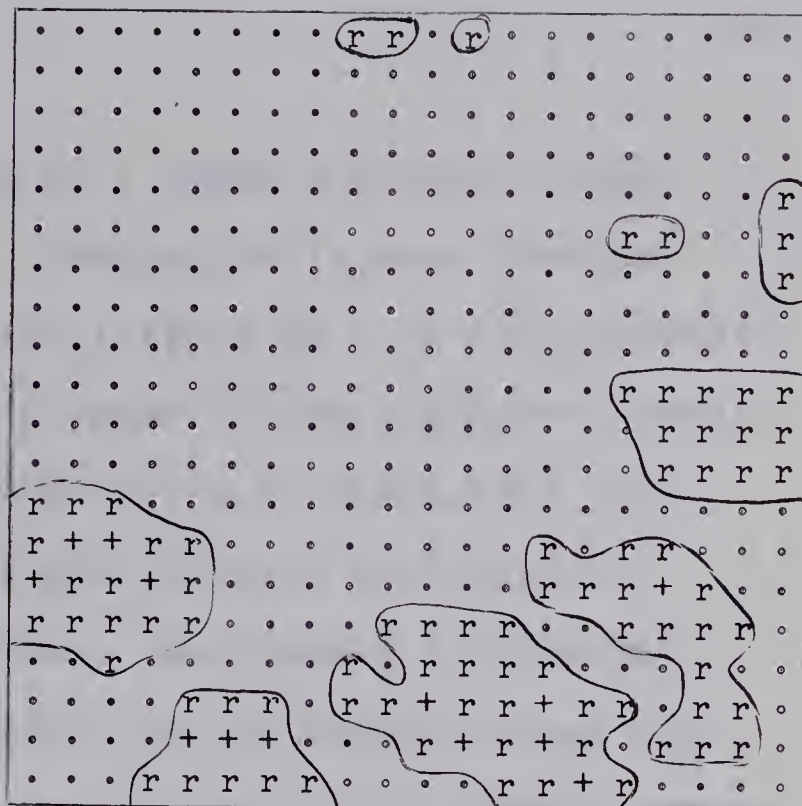


FIGURE 32

Pyrola secunda

41-B-I

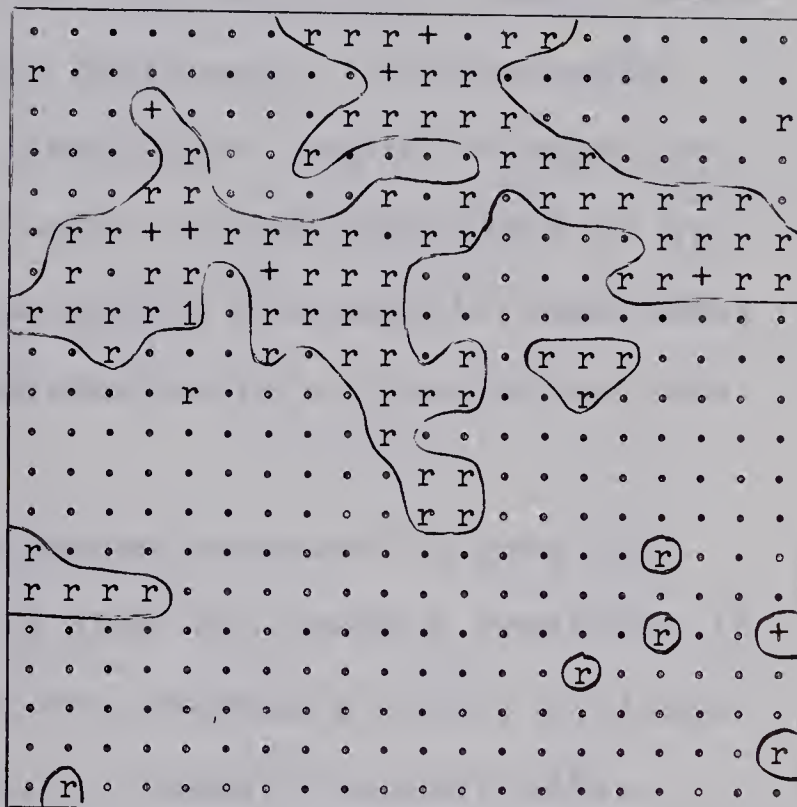
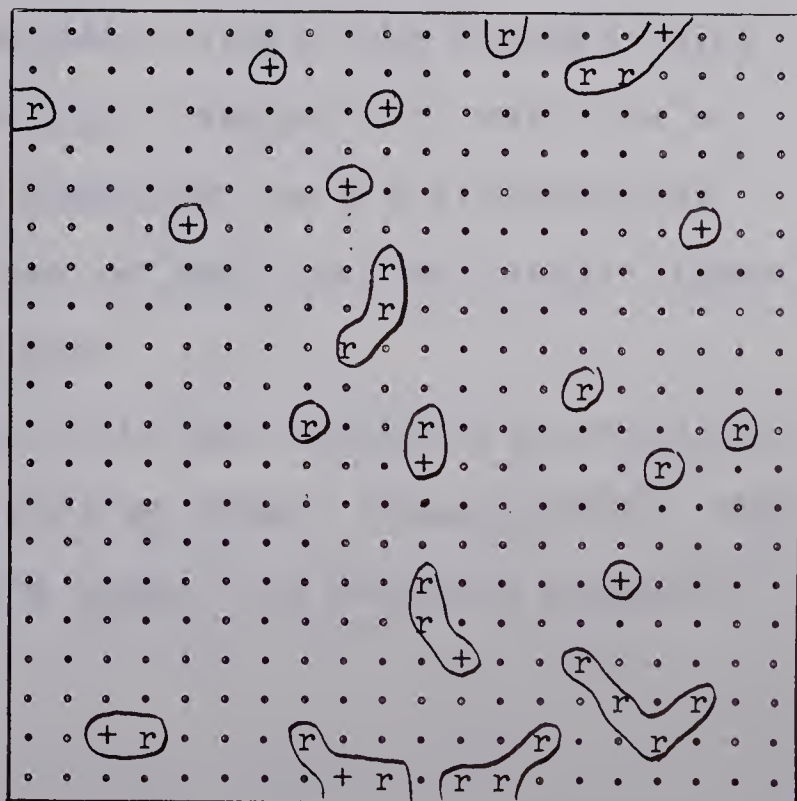


FIGURE 33

Phyllodoce spp.

41-B-I



Shepherdia canadensis (Figure 35) shows a similar though less pronounced correlation. *Shepherdia* is more abundant and more healthy than *Menziesia* (Figure 34) in the apparently drier and more dense area of pine in the southeast corner. By comparing the distribution patterns of *Shepherdia* and *Menziesia* it can be seen that each attains its greatest abundance at different locations. *Shepherdia* is probably near the upper elevational limits of its natural range and thus is not a strong competitor with *Menziesia*. Beil (1966) described *Shepherdia* as having distinctly "low elevation" affinities (52-5,800 ft) in spruce-fir forests of Banff and Jasper. Therefore, *Menziesia* may succeed *Shepherdia* or at least *Shepherdia* would be expected to decrease in importance as this forest matures and succession to a *Picea-Abies* tree stratum occurs.

The distribution of *Pleurozium schreberi* (Figure 37) is similar to that of *Picea* in that the densest areas are in the north and decrease toward the southeast. This indicates that *Pleurozium* thrives better in cooler, moister sites. However, *Pleurozium* is not abundant within the densest thickets of *Picea* and *Abies* where light intensity is very low at ground level. This does not show well on the distribution maps because of the small sizes of the *Picea* and *Abies* clumps relative to that of the quadrats.

Cornus canadensis (Figure 31) has a distribution pattern which is restricted to the areas of denser *Picea* growth. Why *Cornus* is so restricted is not known. It was most abundant

FIGURE 34

Menziesia glabella

41-B-I

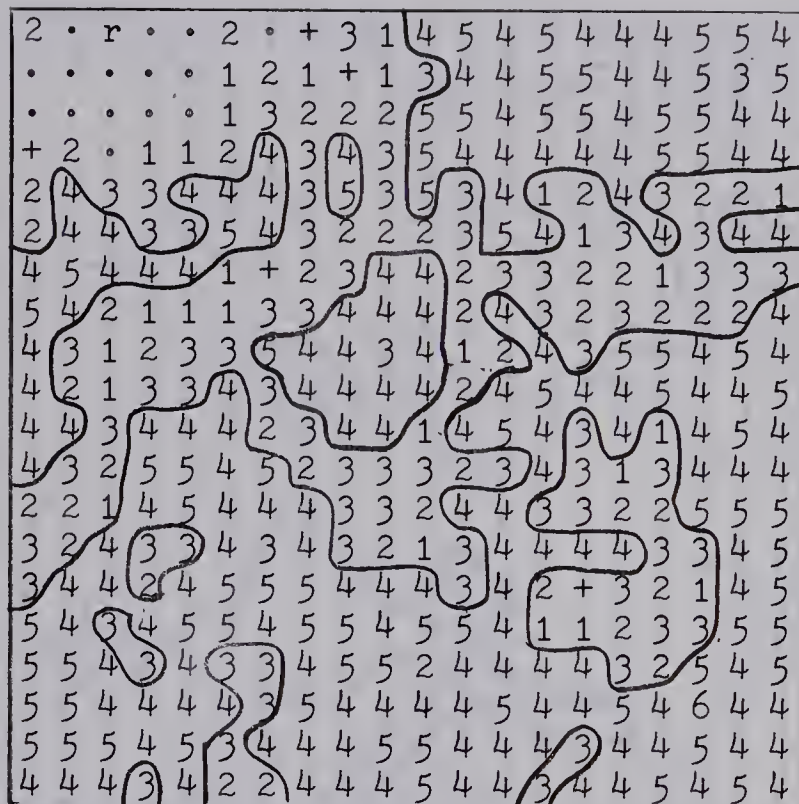


FIGURE 35

Shepherdia canadensis

41-B-I

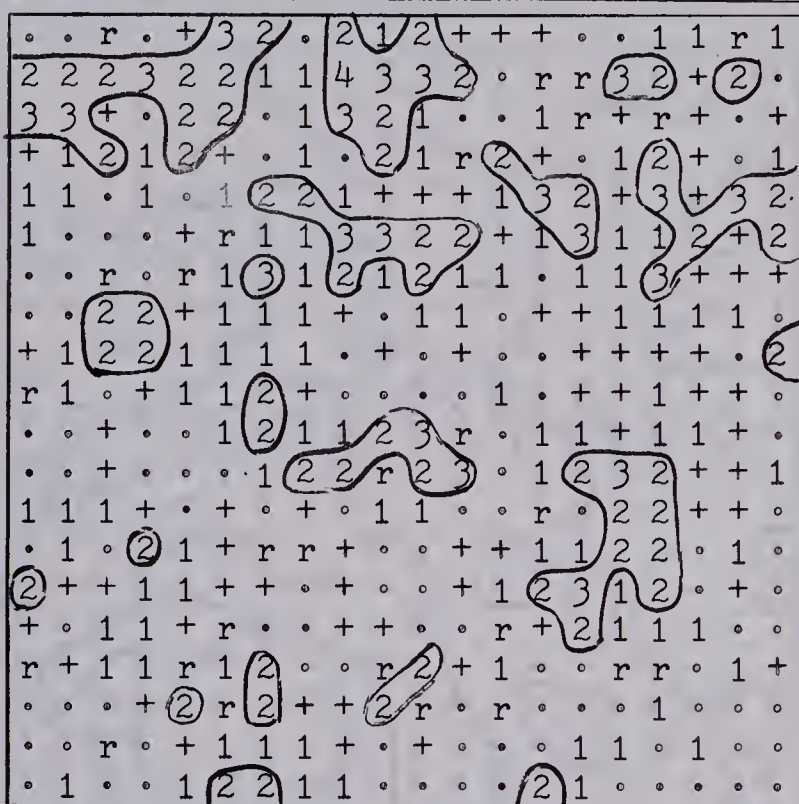


FIGURE 36

Vaccinium scoparium

41-B-I

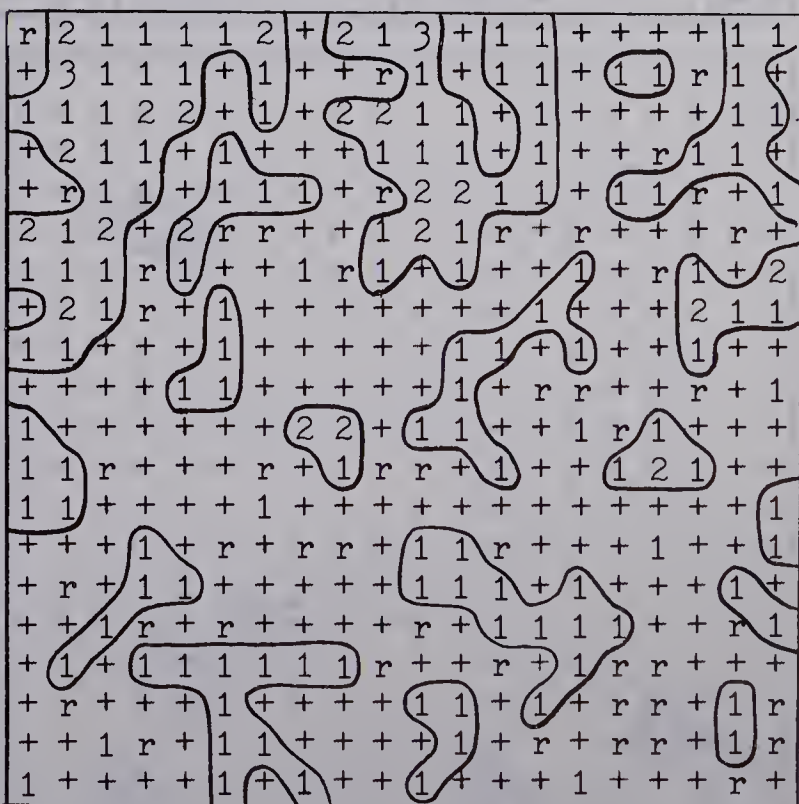


FIGURE 37

Pleurozium shreberi

41-B-I

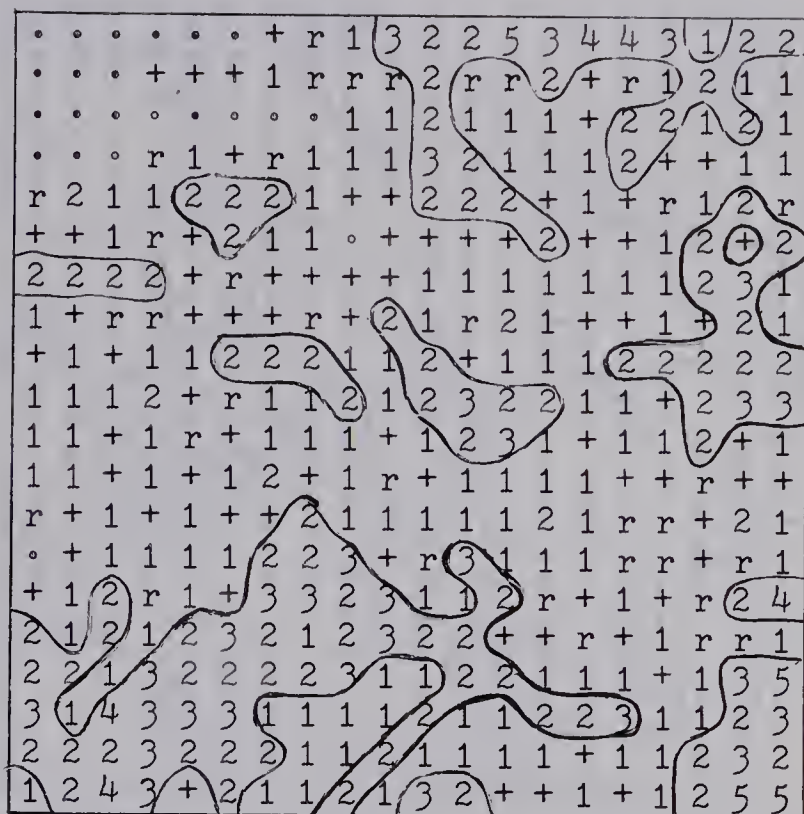


FIGURE 38

Ptilium crista-castrensis

41-B-I

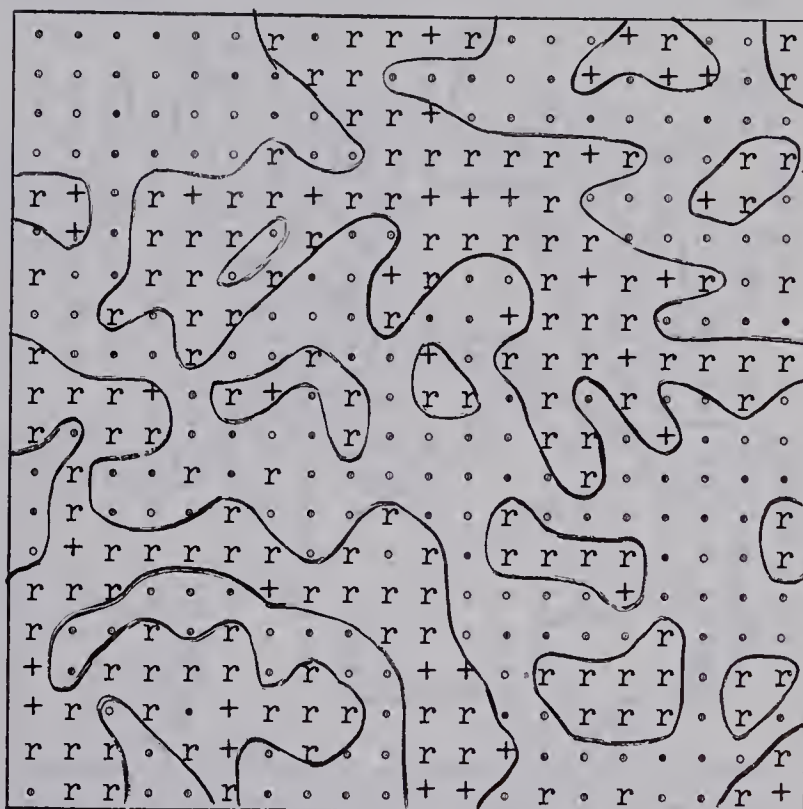


FIGURE 39

Hylocomium splendens

41-B-I

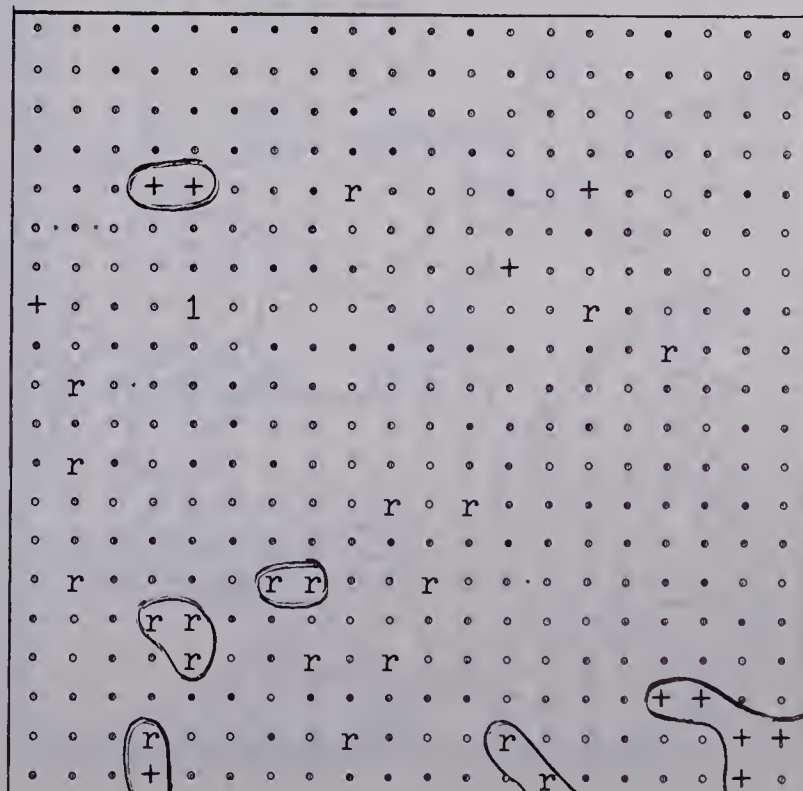


FIGURE 40

Arnica cordifolia

41-B-I

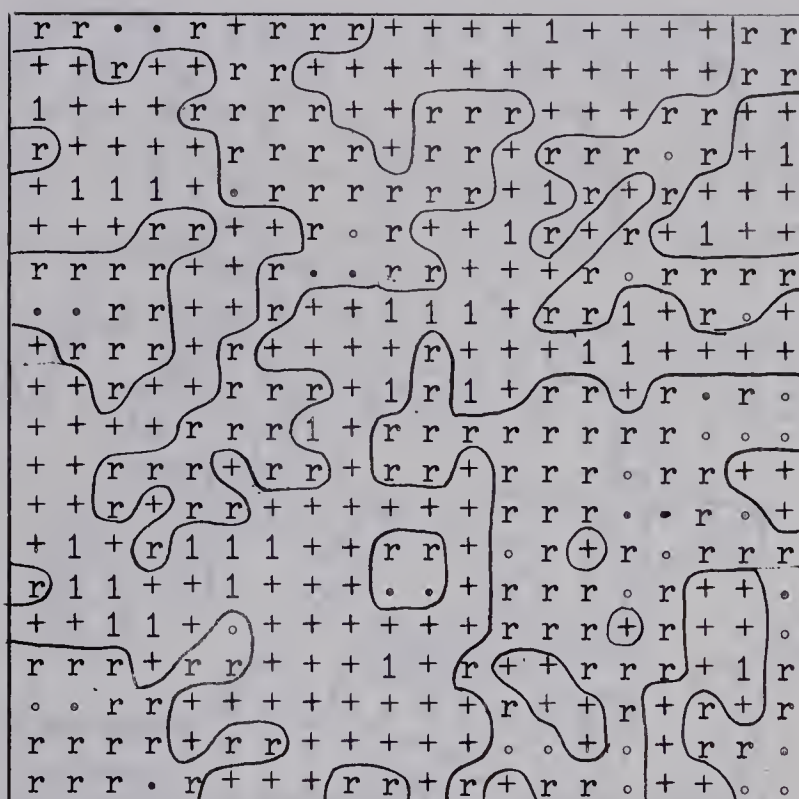


FIGURE 41

Carex spp.

41-B-I

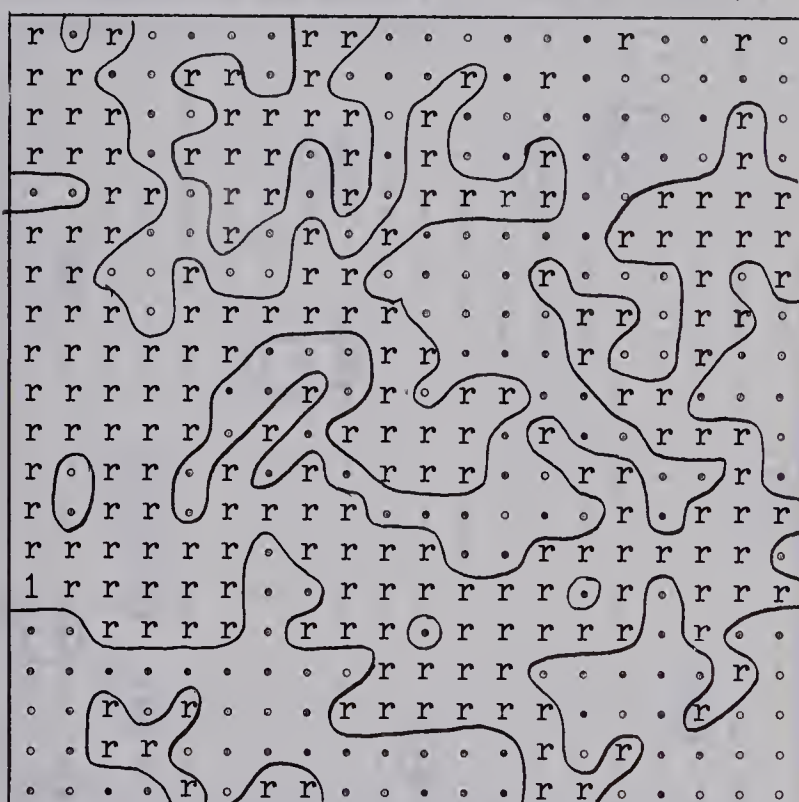


FIGURE 42

Linnaea borealis

41-B-I

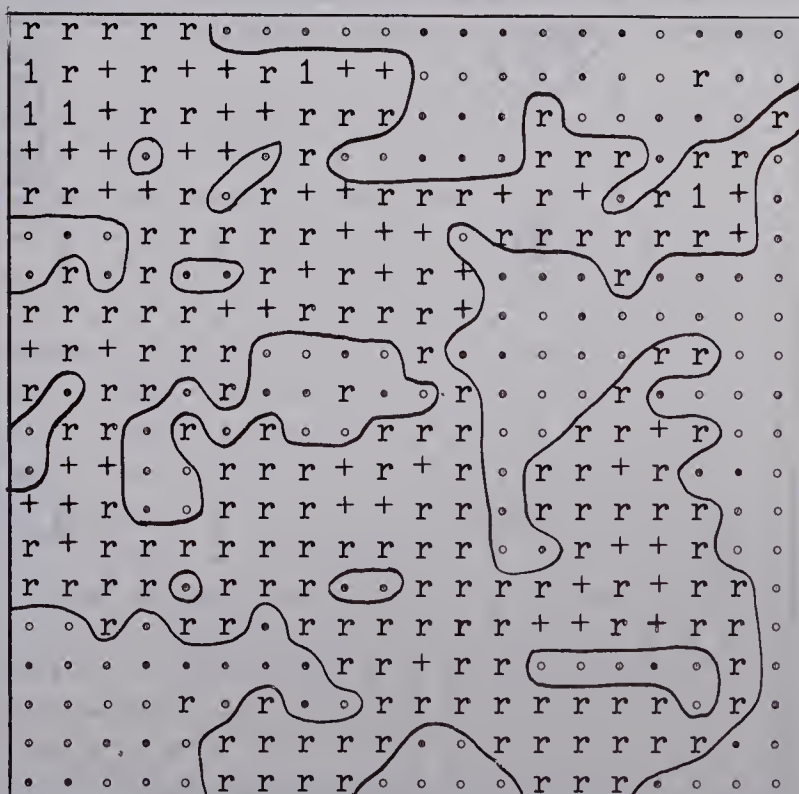


FIGURE 43

Epilobium angustifolium

41-B-I

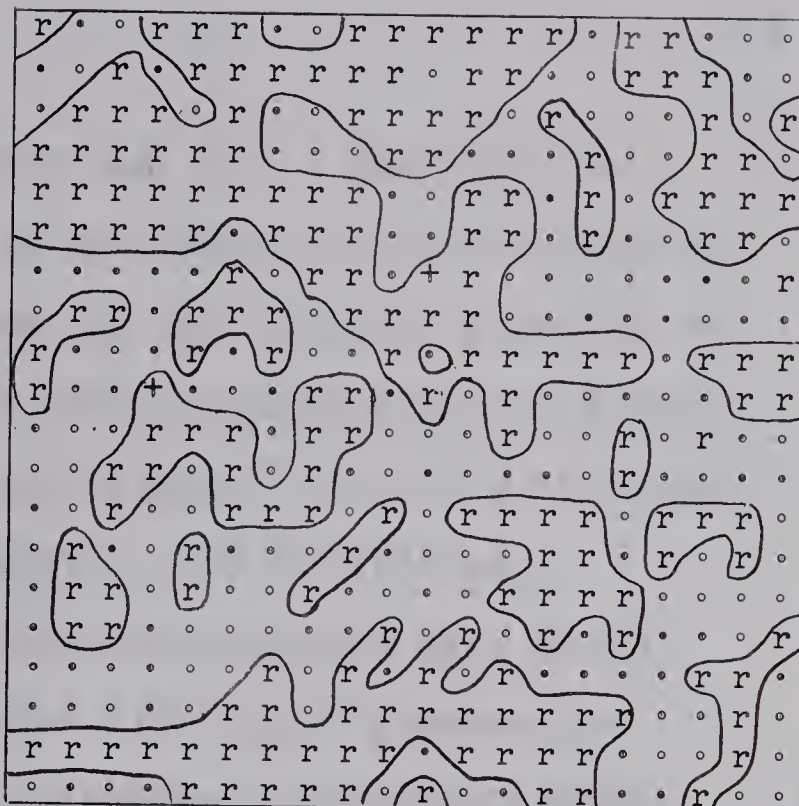


FIGURE 44

Rhododendron albiflorum

41-B-I

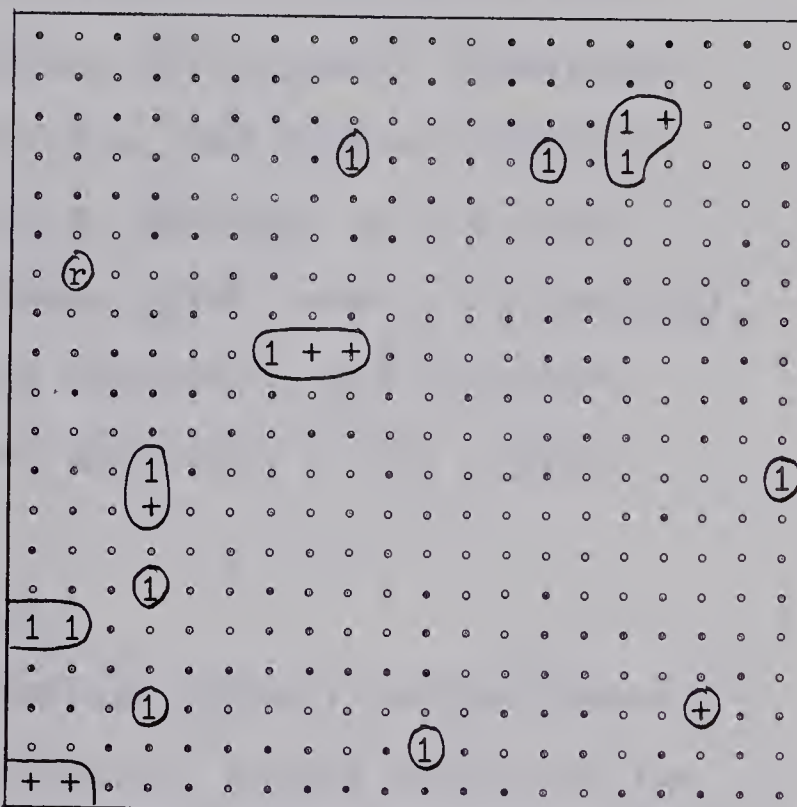
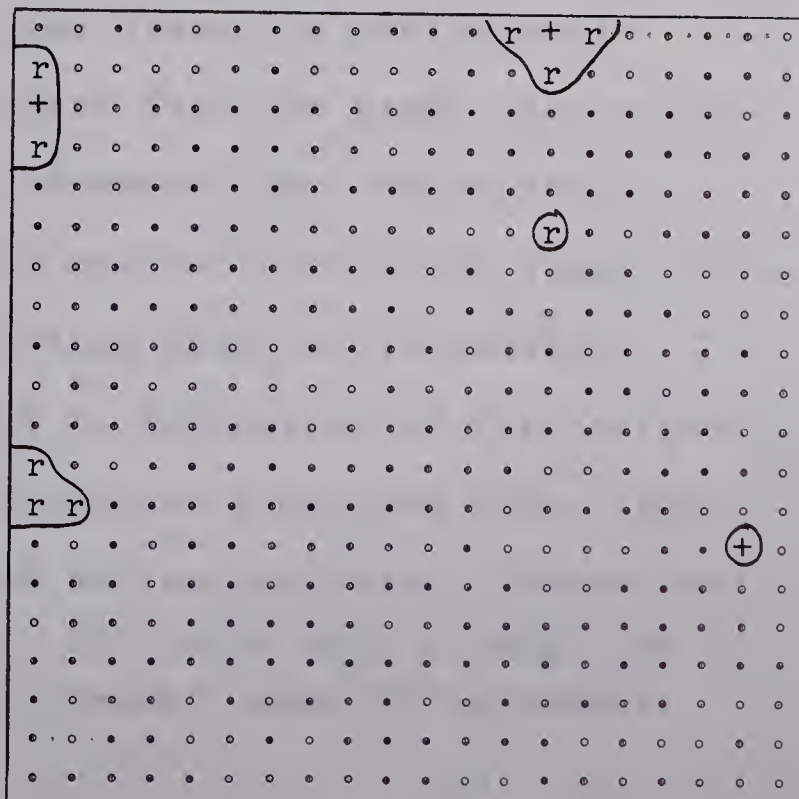


FIGURE 45

Spiraea lucida

41-B-I



in cool, moist stands like 38-B and 26-J. The moisture gradient across this stand did not appear to be so steep as to exclude *Cornus* from the central and southern portions of the plot, especially when the wider distributions of *Pyrola secunda* and *Ledum groenlandicum* (Figures 32, 47) with which *Cornus* is often closely associated, are considered.

Although not evident in the distribution maps based upon 5 x 5 m quadrats, the dense high-shrub stratum has a strong influence upon the distribution of smaller plants. For example, *Vaccinium scoparium*, *Stereocaulon tomentosum*, *Cladonia ecmocyna*, *Linnea borealis*, and *Arnica cordifolia*, amongst others, are restricted to openings in the shrub stratum or to areas of less dense shrub cover. In contrast, *Carex concinnoides*, *Pleurozium schreberi*, and *Peltigera aphthosa* do best beneath or at the edges of the shrubs.

2. STAND 47-B-I: TREE STRATUM

Figure 55 shows a decreasing gradient in pine density from the southwest to the northeast. Aerial photos of the entire forest show that the pine trees are contagiously distributed in clumps much larger than the study plot which is located across the border of one of the denser areas. The reasons for this contagion are not positively known but the following hypotheses are based upon the information available. The present forest is definitely of fire origin and was preceded by a mixed forest of *Picea* and *Pinus* (the presence of *Abies* is suspected but not certain). Since this prior forest was approximately 225 years old, it might be assumed that the pines, while present, were not abundant.

FIGURE 46

Lonicera involucrata

41-B-I

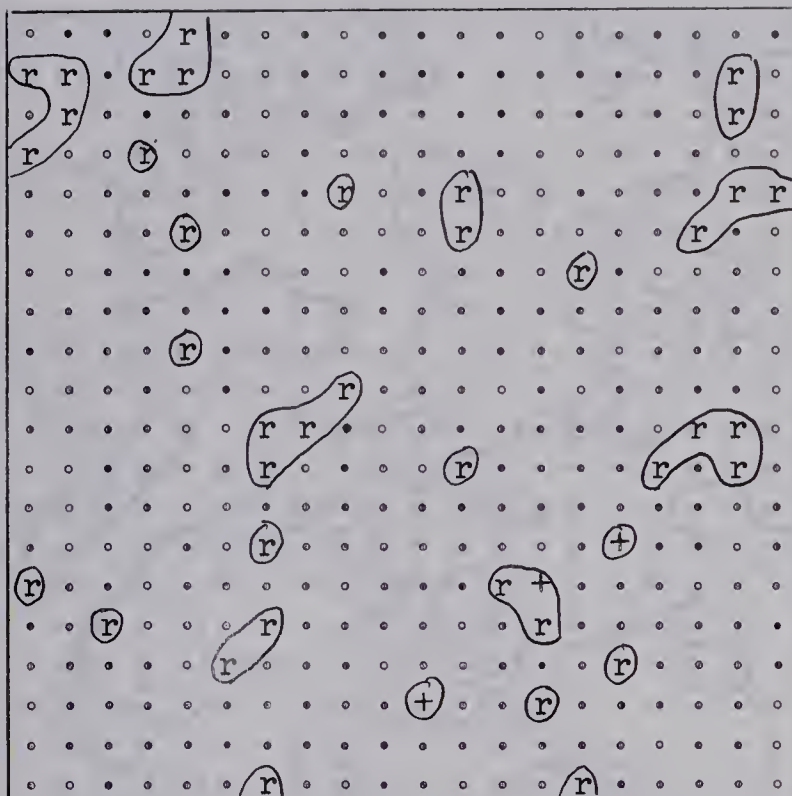


FIGURE 47

Ledum groenlandicum

41-B-I

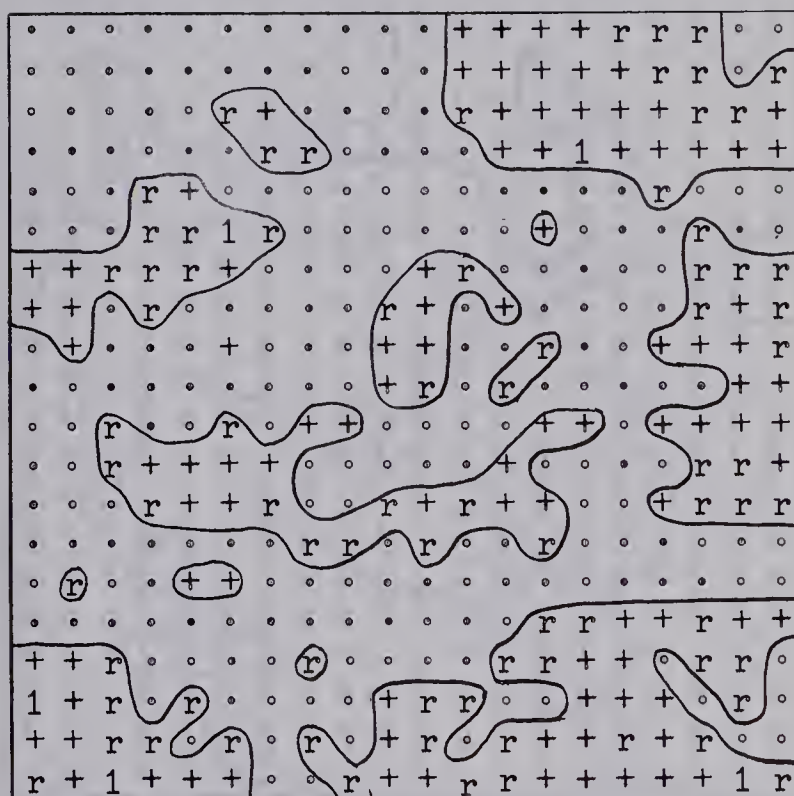
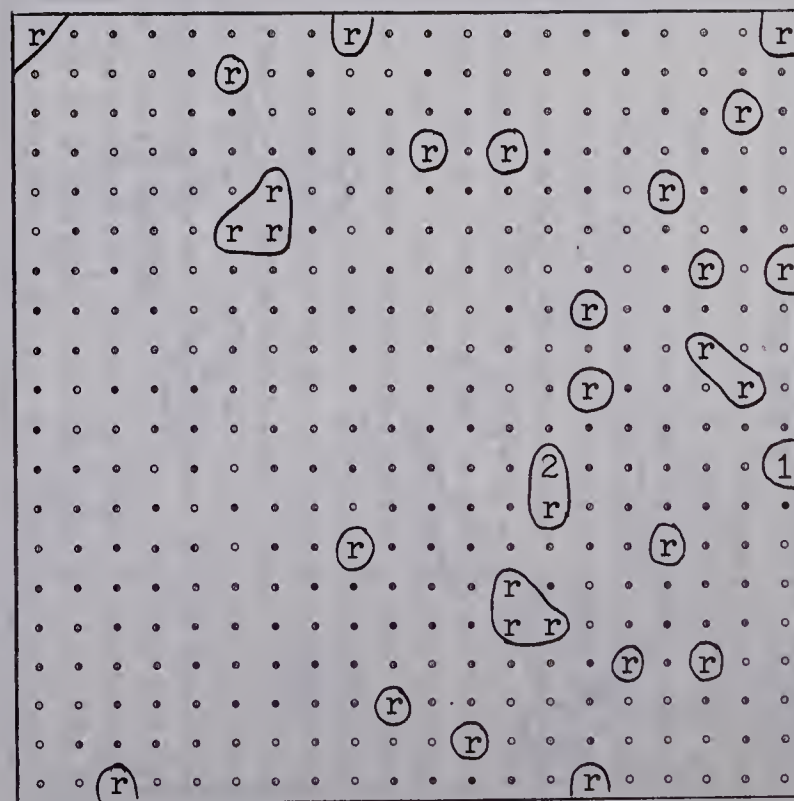


FIGURE 48

Salix spp.

41-B-I





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FIGURE 49

Stereocaulon tomentosum

41-B-I

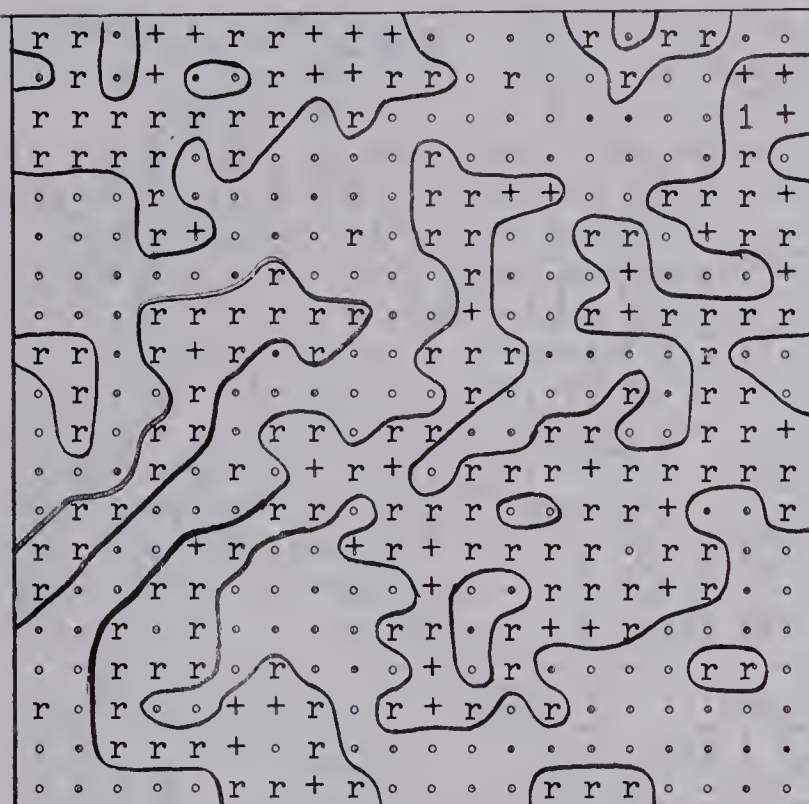


FIGURE 50

Cladonia spp.

41-B-I

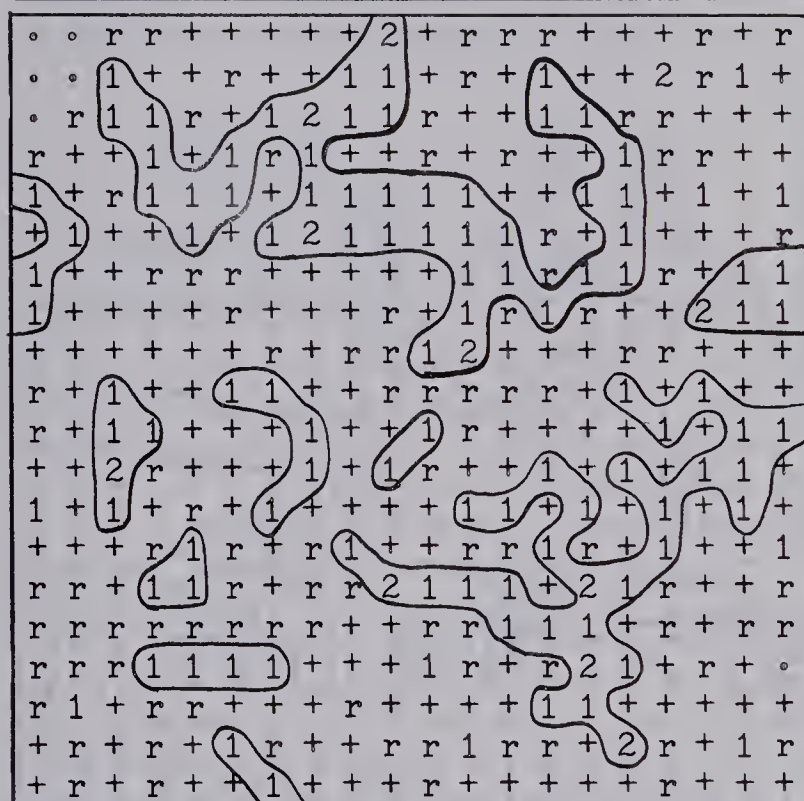


FIGURE 51

Peltigera spp.

41-B-I

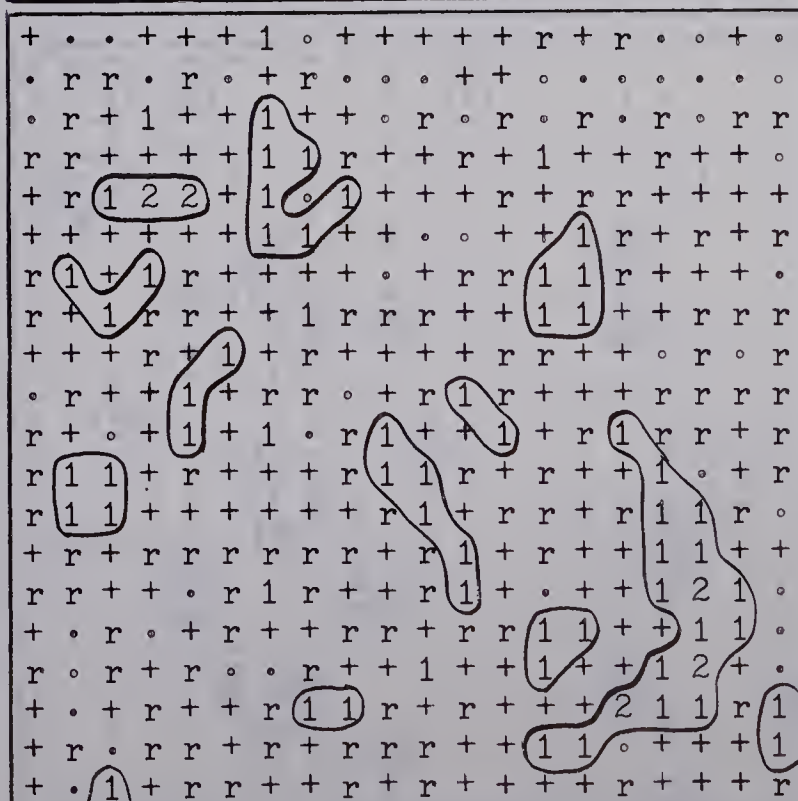




Figure 1
Topographic map of the study area
Scale: 1:50,000



Figure 2
Topographic map of the study area
Scale: 1:50,000



Figure 3
Topographic map of the study area
Scale: 1:50,000

FIGURE 52

Polytrichum juniperinum

41-B-I

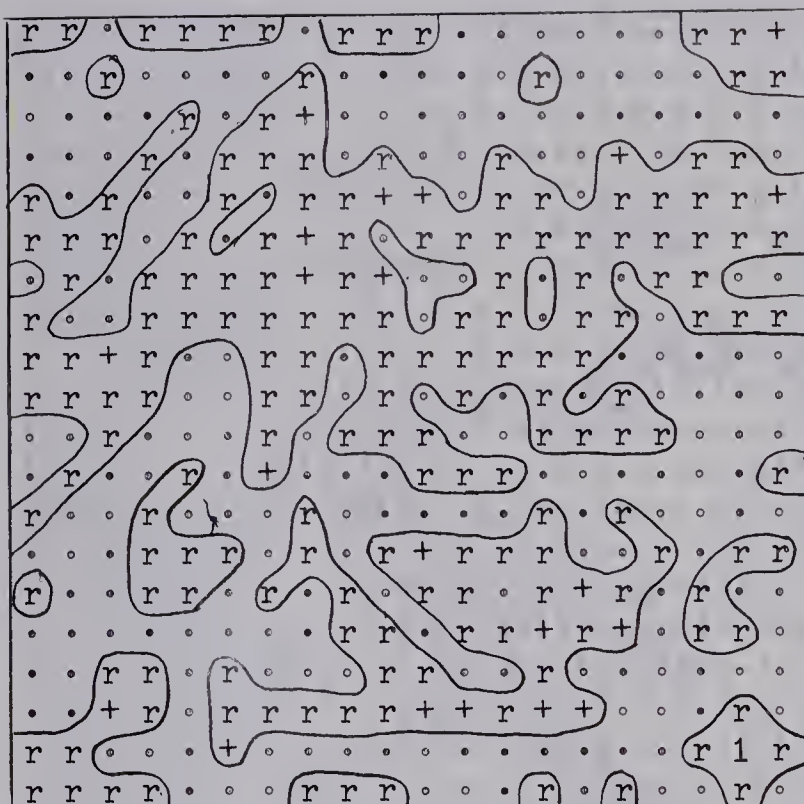


FIGURE 53

Dicranum polysetum

41-B-I

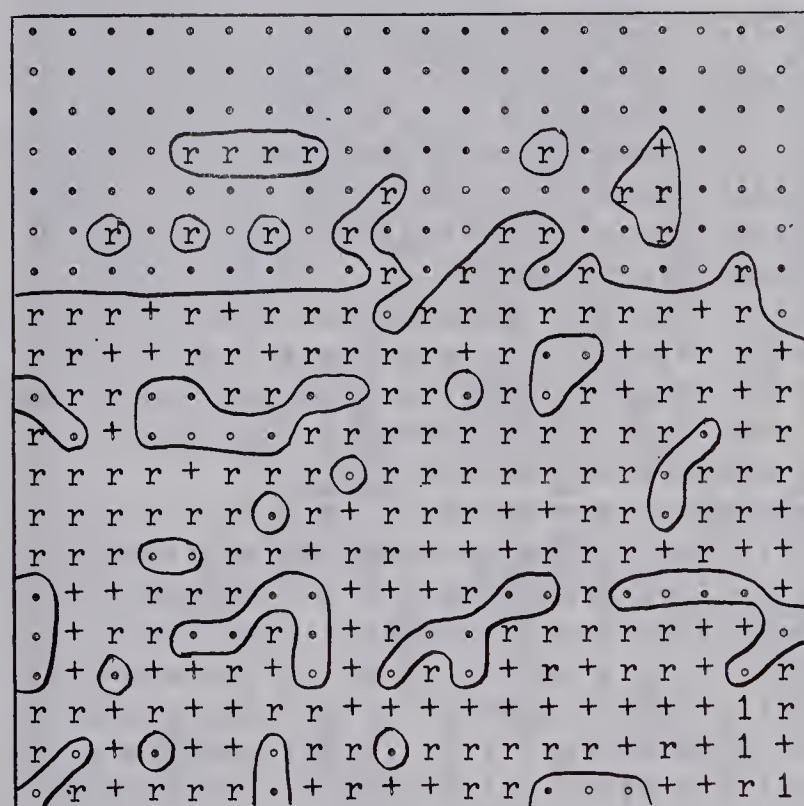


FIGURE 54

Juniperus communis

41-B-I

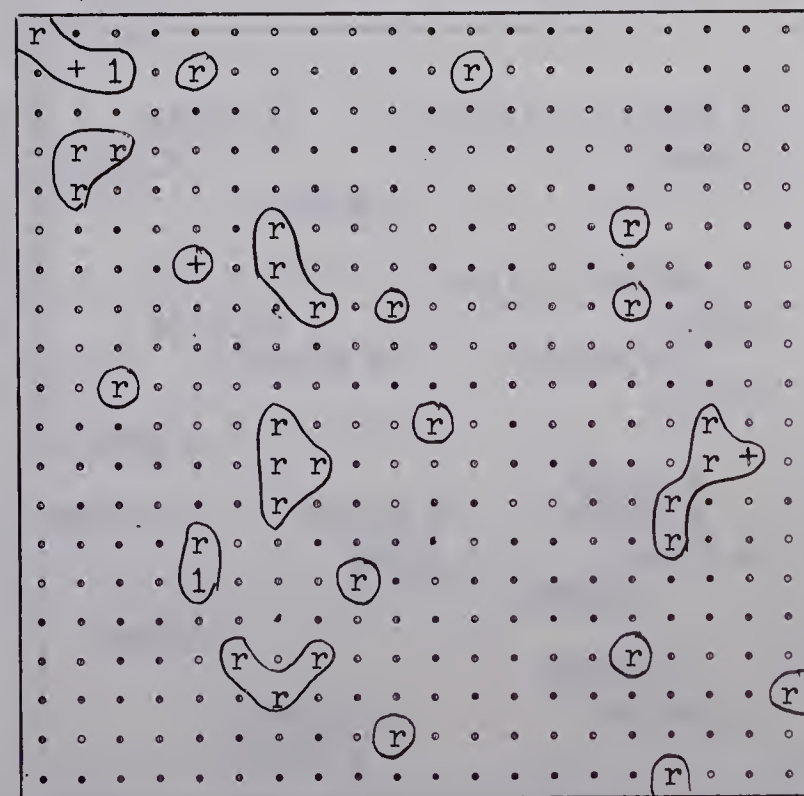


FIGURE 55

47-B-I

Pinus contorta

trees

1= 1-3 individuals
 2= 4-5 individuals
 3= 6-8 individuals
 4= 9-19 individuals
 5= more than 19
 individuals

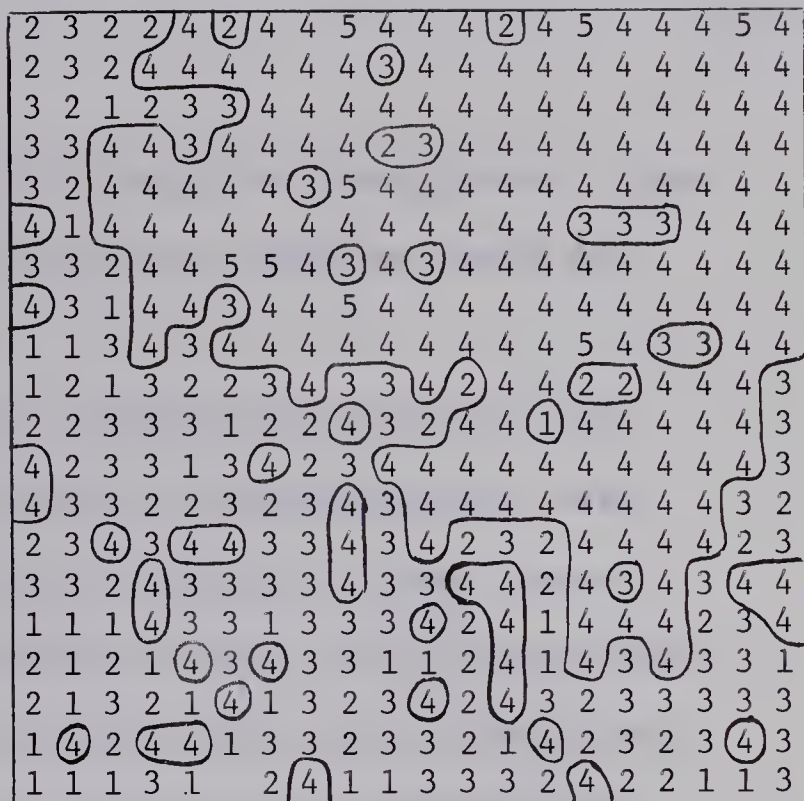


FIGURE 56

47-B-I

deadfall distributions

l= low cover
 m= medium cover
 h= high cover

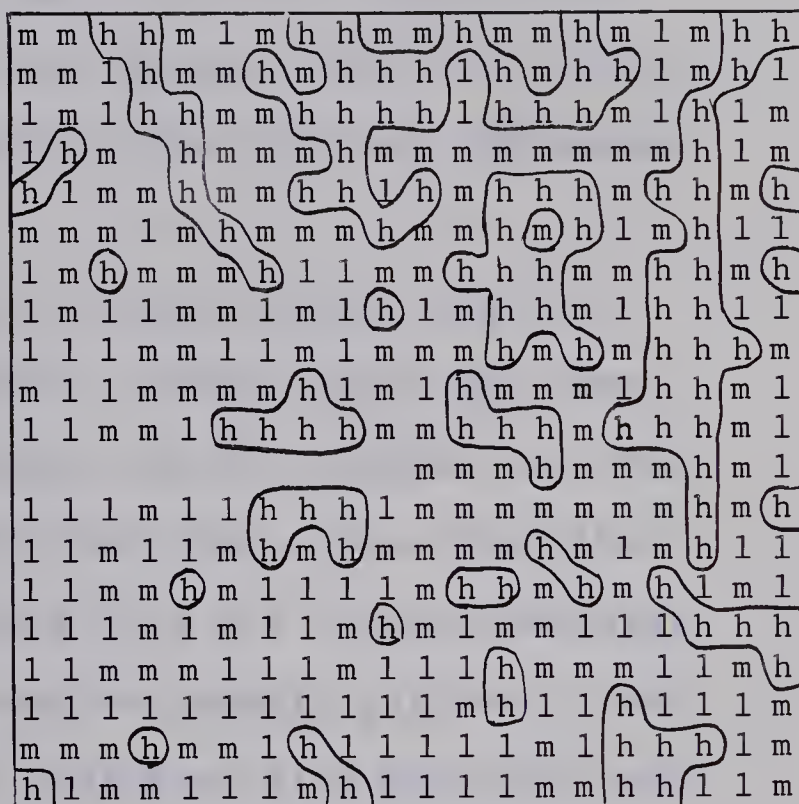
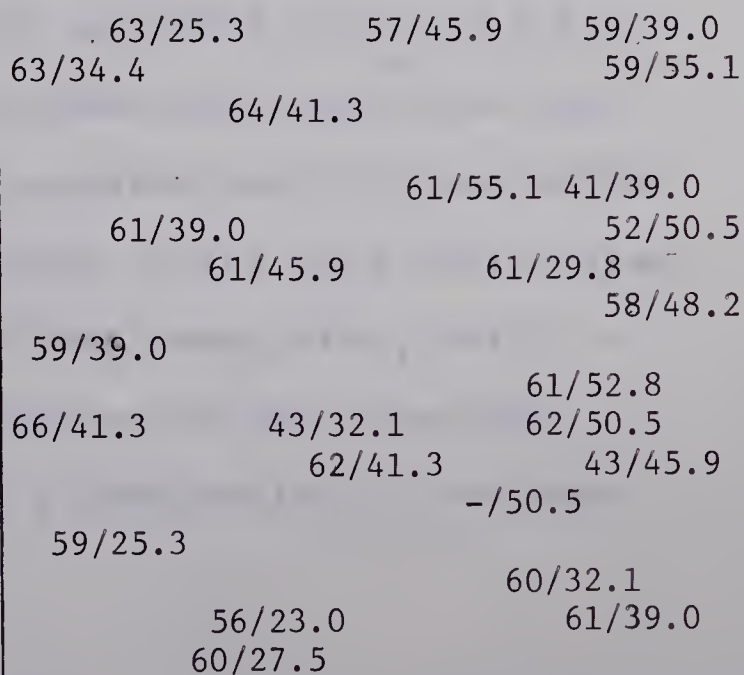


FIGURE 57

47-B-I

age/basal area
 (m^2 / hectare)



The distribution of seed from these trees following fire would be contagious. Thus the differences in present levels of stocking could be accounted for.

It is also possible that different potentials for pine seedling establishment existed throughout the area such that seedling mortality was greater in some areas than others. What factors would account for this variable potential are not known, but could relate to differences in available water in the surface soil, or competition between the pine and other early pioneer species, or any of a number of factors present in the past but not measurable in the present.

The deadfall distribution illustrated in Fig. 56 shows the same density gradient. Since nearly all trees of the prior forest have fallen, and the deadfall is comprised almost entirely of pre-fire trees, this distribution of deadfall would indicate that the forest preceding the present may have had a similar density pattern. This would support the hypothesis that some site factor(s) was operative which affected tree density.

Basal area shows a similar gradient across the plot (Fig. 57). Unfortunately this does not favour one hypothesis over the other. This gradient may indicate either a lower potential for pine growth in the less dense area or incomplete stocking of the less dense area, which is plausible considering the young age of the stand (60 years), or it could represent a combination of the two.

There is some indirect evidence that the entire stand is fully stocked at present. Figure 58 shows a slightly greater density of pine seedlings in the less dense area of pine trees, but the gradient of seedling density may be related to the deadfall distribution--where heavy, the dead fall greatly reduces the area of potential sites for seedling germination. (Note, only that portion of dead fall in direct contact with the ground is actively decomposing.) Despite the fact that pine seeds are germinating, the survival rate is practically nil as only five sapling size pines were found in the entire plot. Unless it is assumed that these saplings represent a sudden, new wave of pine regeneration, then it is obvious that the stand is fully stocked and no new pines are becoming established.

Picea engelmannii appears to have begun to seed this area about 20 years after the fire. Two trees cored yielded ages of 43 and 46 years respectively (at 4.5 ft above ground). Most of the tree-sized individuals are in the 7.5 - 15 cm size class although a few are in the next largest class, *i.e.* 15 - 23 cm. These individuals appear to be fairly evenly distributed across the plot (Fig. 59). Although the *Picea* seedlings are also fairly evenly distributed (Fig. 60), the sapling-sized *Picea* are somewhat denser towards the southwest (Fig. 61). A chi-square test of geographic homogeneity (Cottam, Curtis, and Hale 1953) for the *Picea* saplings yields a

FIGURE 58

47-B-I

Pinus contorta
seedlings

numbers = actual
numbers of individuals.

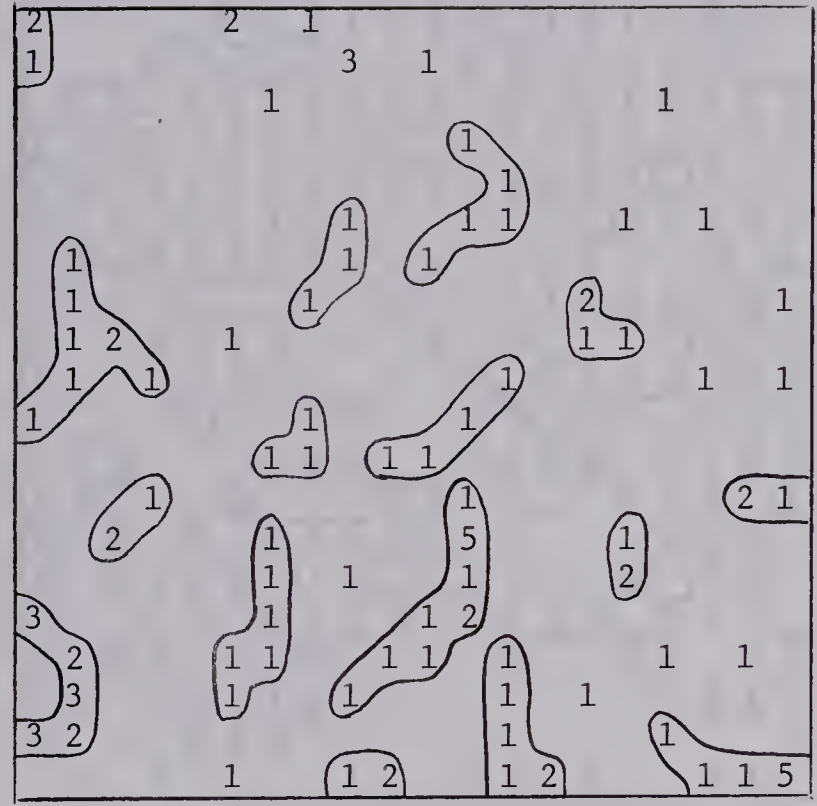


FIGURE 59

47-B-I

Picea engelmannii
trees

1= 1 individual
2= 2 individuals
3= 3-4 individuals

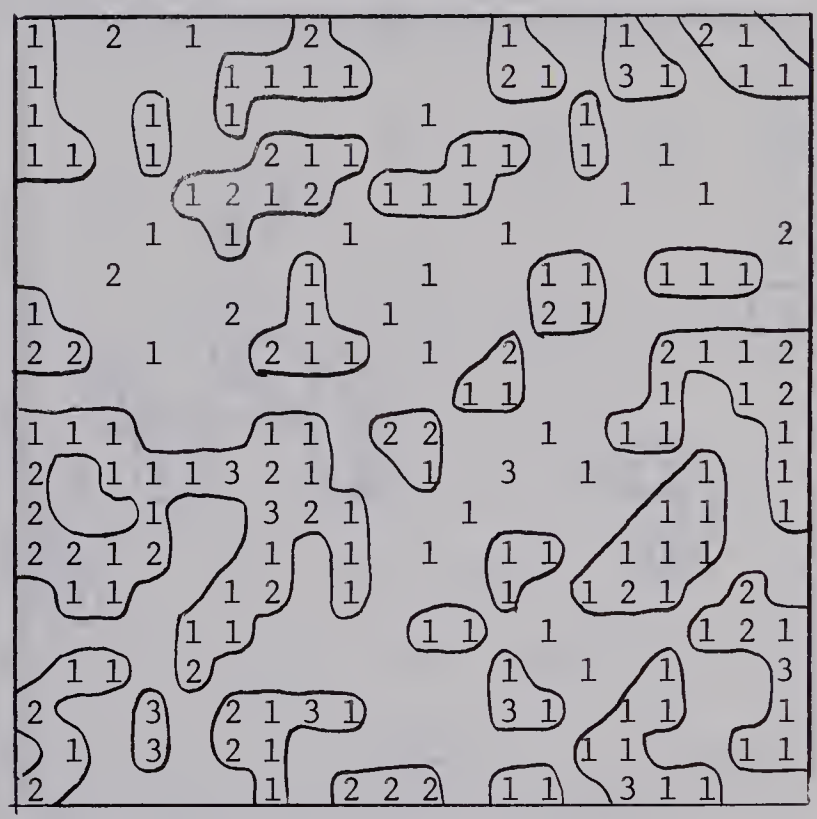


FIGURE 60

47-B-I

Picea engelmannii
seedlings

numbers = actual
numbers of individuals.

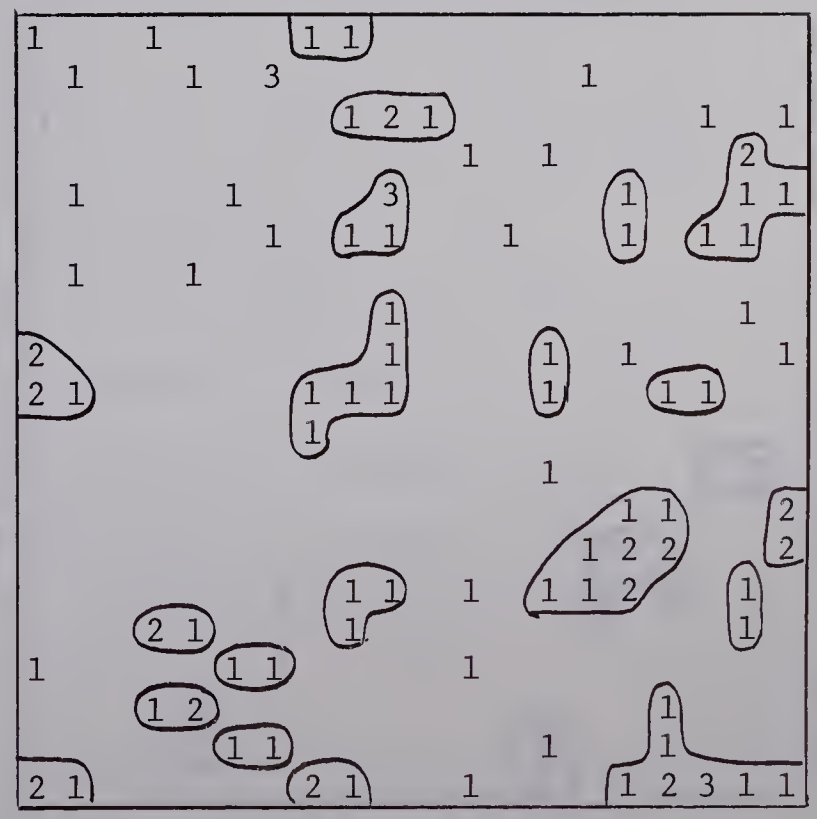




PLATE 1
 FISH
 DRAWINGS BY J. H. HARRIS
 1891



PLATE 2
 FISH
 DRAWINGS BY J. H. HARRIS
 1891

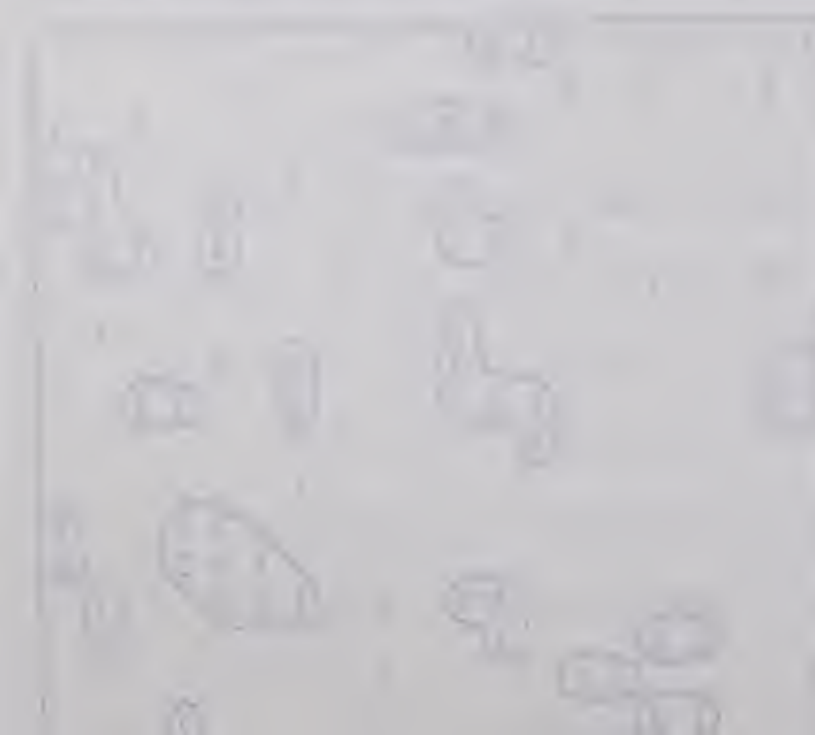


PLATE 3
 FISH
 DRAWINGS BY J. H. HARRIS
 1891

FIGURE 61

47-B-I

Picea engelmannii
saplings

1= 1 individual
2= 2 individuals
3= more than 2
individuals.

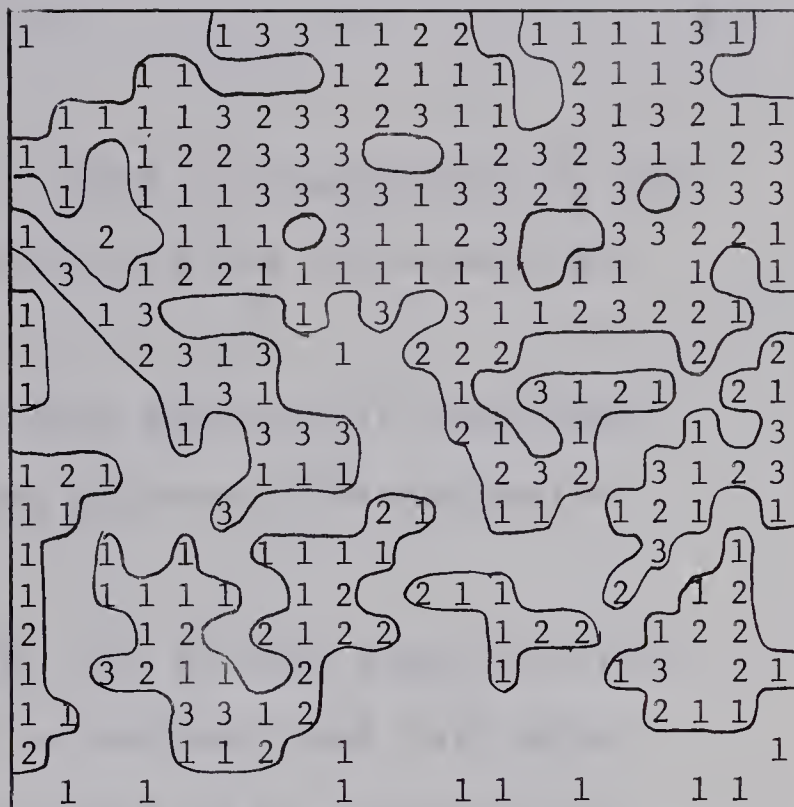


FIGURE 62

47-B-I

Abies lasiocarpa
seedlings

numbers = actual
numbers of individuals.

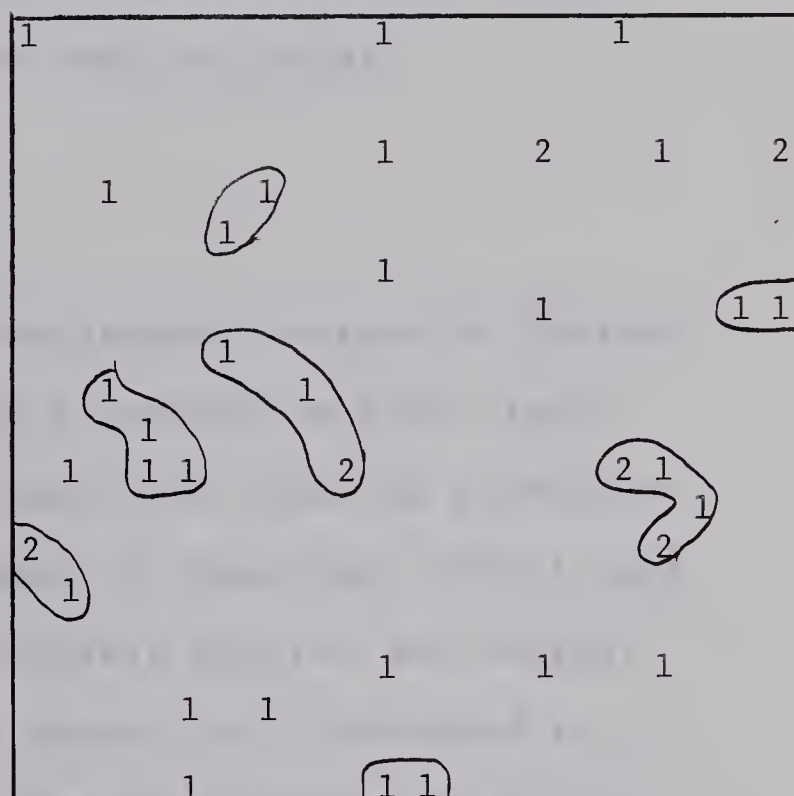
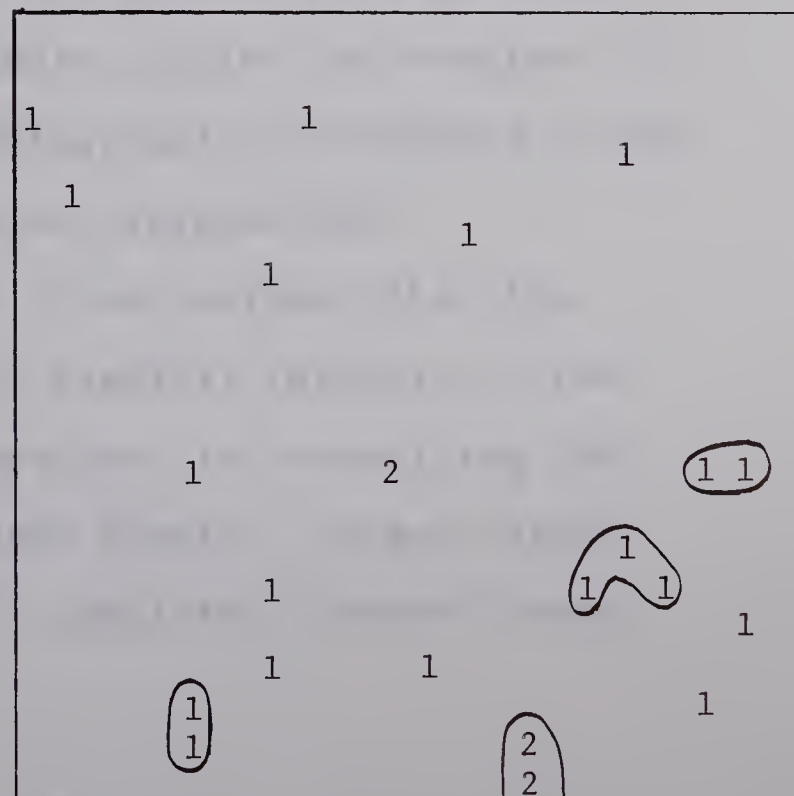


FIGURE 63

47-B-I

Abies lasiocarpa
saplings

numbers = actual numbers
of individuals.





1. Subject

1-3-73

1. Subject
1-3-73

1. Subject 1-3-73

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1. Subject

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1. Subject

1-3-73

1. Subject 1-3-73

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1. Subject 1-3-73

chi-square of 77.3 (23 d.f.), which is significant at the 1% level. This shows that the *Picea* are not evenly distributed across the plot.

Abies lasiocarpa is not very abundant in the stand and as yet shows no particular pattern of distribution (Fig. 62 and 63).

Considering the age (Fig. 57) of this stand and the great abundance of *Picea*, it is obvious that this pine forest, like 41-B-I, is seral and will be succeeded by *Picea* with some *Abies* if fire does not occur.

THE SUBORDINATE STRATA

There is no prominent topographic feature to control the distribution of subordinate species in this stand. The slight gradient of tree densities from the southwest to the northeast does not appear to have much effect upon the distribution of the subordinate species and neither does the density of the tree canopy as illustrated in Fig. 64. Nevertheless, when the distribution of Cover-Abundance classes of subordinate species are examined, it is apparent that they are contagiously distributed in the area, perhaps due to vegetative reproduction.

From field observations it was evident that the abundance and distribution of deadfall (primarily from the previous forest) were important in controlling the distribution of the subordinate plants. In many areas deadfall was so thick that it completely covered large

areas of ground, thus physically excluding or reducing the sizes of many plant populations. With decay being relatively slow for wood not in direct contact with the ground, this condition will persist for a long time. Although notes were made in each quadrat concerning the abundance of deadfall, it was found that the quadrat size was too large and the abundance scale too coarse to allow useful correlations to be made with subordinate species distributions.

The trees exhibit at least two scales of distribution pattern: (1) the gradient of density, (2) an aggregation into small clumps. The understory vegetation is often very sparse within these clumps, and much of the ground is covered only by needle litter in these areas. Because these clumps are few in number (primarily on the north and northeast sides of the plot) and often smaller than a single quadrat, their effect upon the subordinate strata is not noticeable on the distribution maps.

Although not pronounced, the following patterns are notable. *Lycopodium complanatum* (Fig. 65) and *Stereocaulon tomentosum* (Fig. 70) occur primarily in the northeast area with the lower tree density, whereas *Equisetum scirpoides* (Fig. 72) and *Ledum groenlandicum* are more abundant (Fig. 73) and *Linnaea* (Fig. 75) less abundant in the more densely treed southwest area of the plot. This latter area is in an elongated and shallow depression (Fig. 13) and may be slightly moister than surrounding areas. *Arnica*

FIGURE 65

Lycopodium complanatum

47-B-I

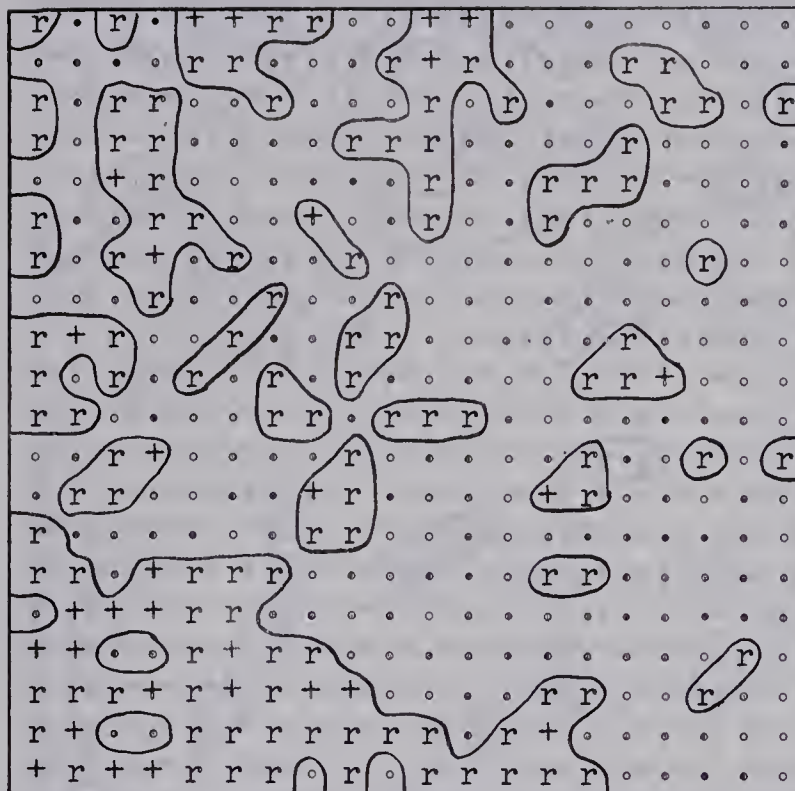


FIGURE 66

Lycopodium annotinum

47-B-I

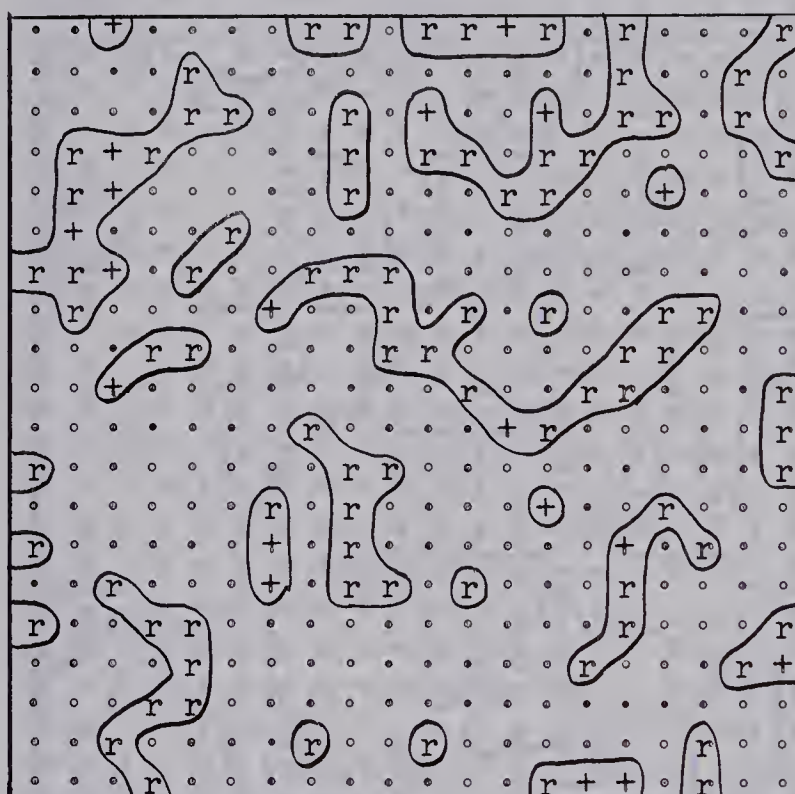


FIGURE 67

Goodyera oblongifolia

47-B-I

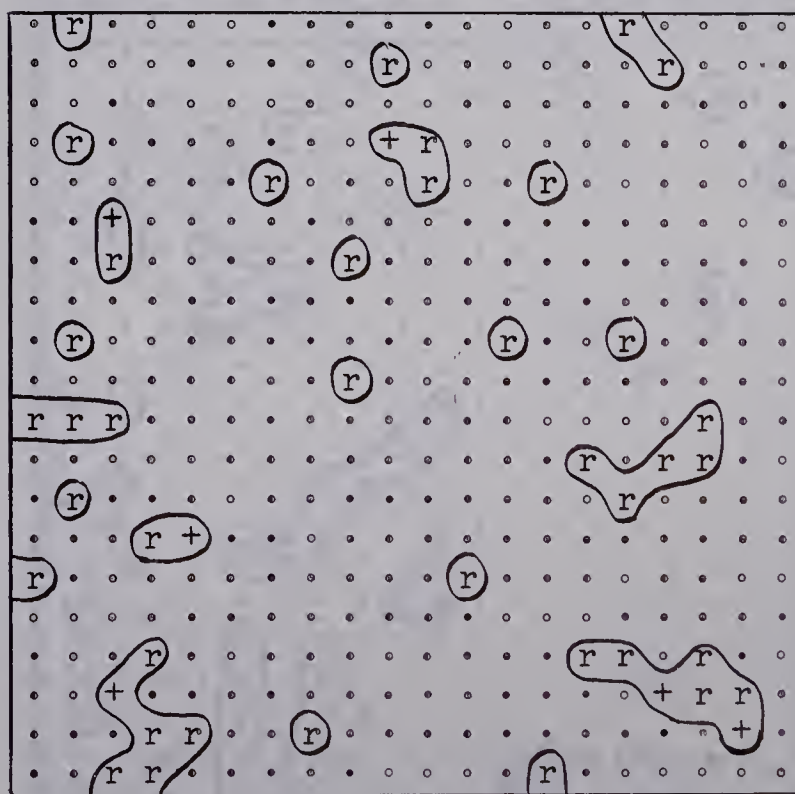


FIGURE 68

Peltigera spp.

47-B-I

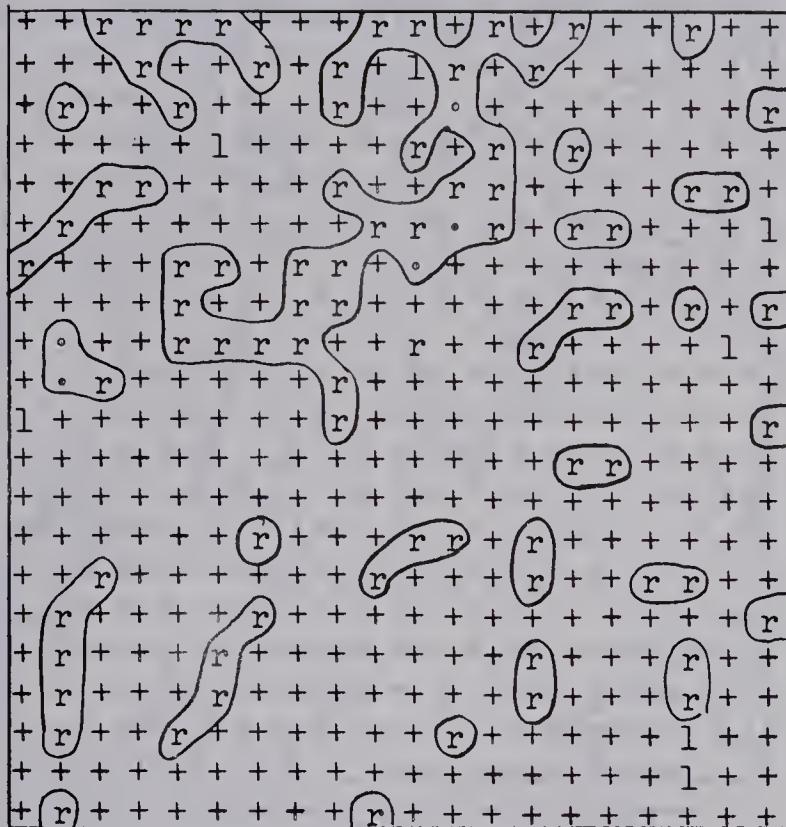


FIGURE 69

Cladonia spp.

47-B-I

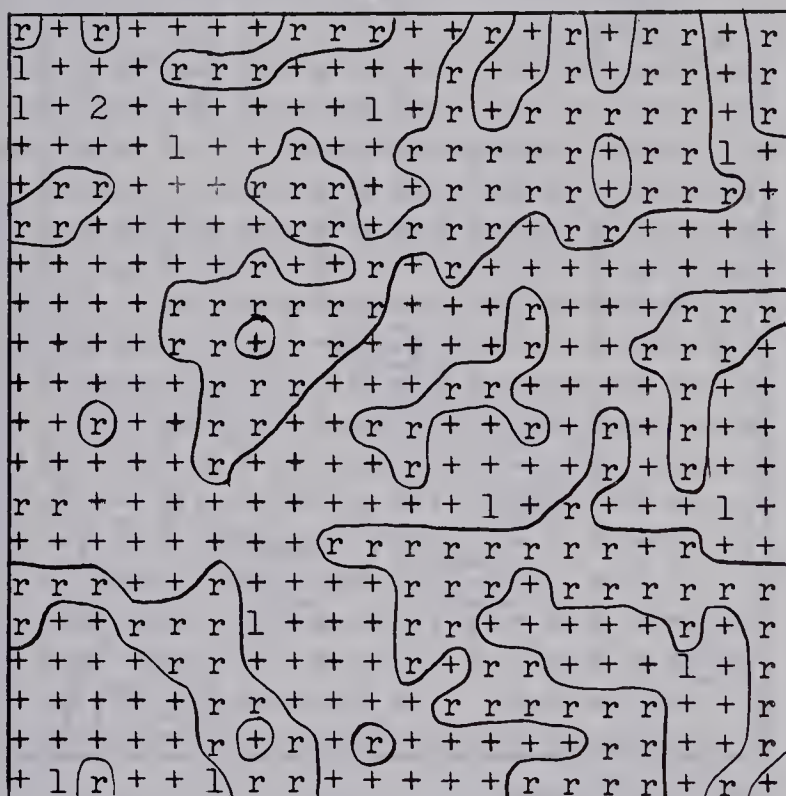


FIGURE 70

Stereocaulon tomentosum

47-B-I

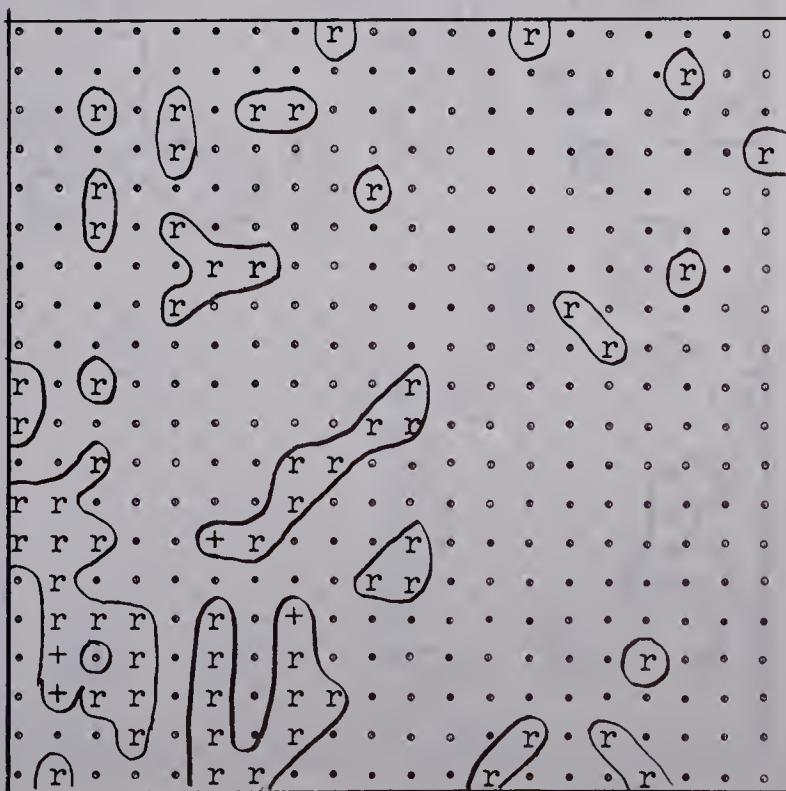


FIGURE 71

Lonicera involucrata

47-B-I

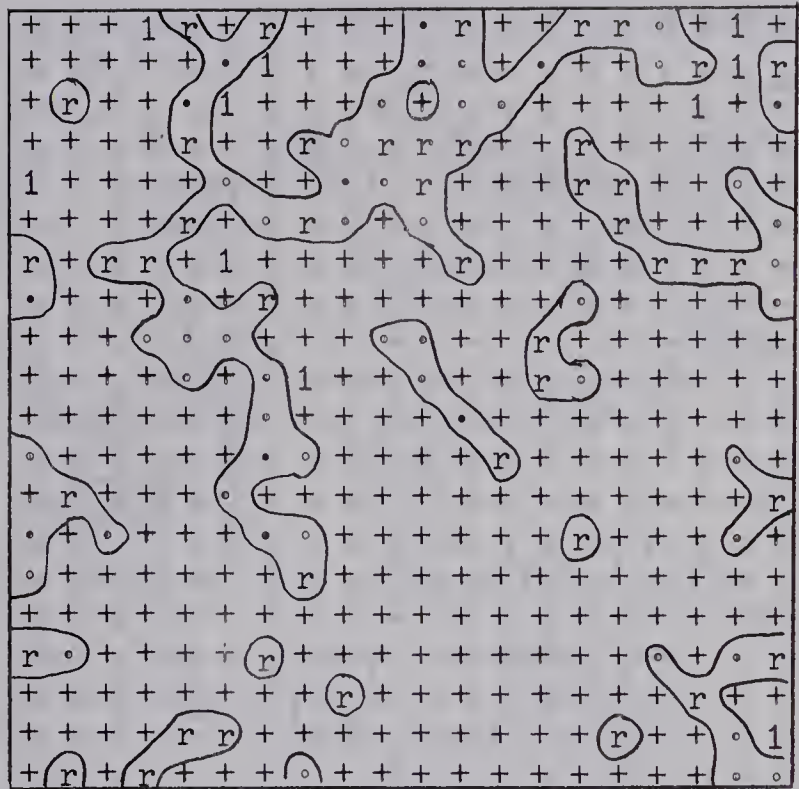


FIGURE 72

Equisetum scirpoides

47-B-I

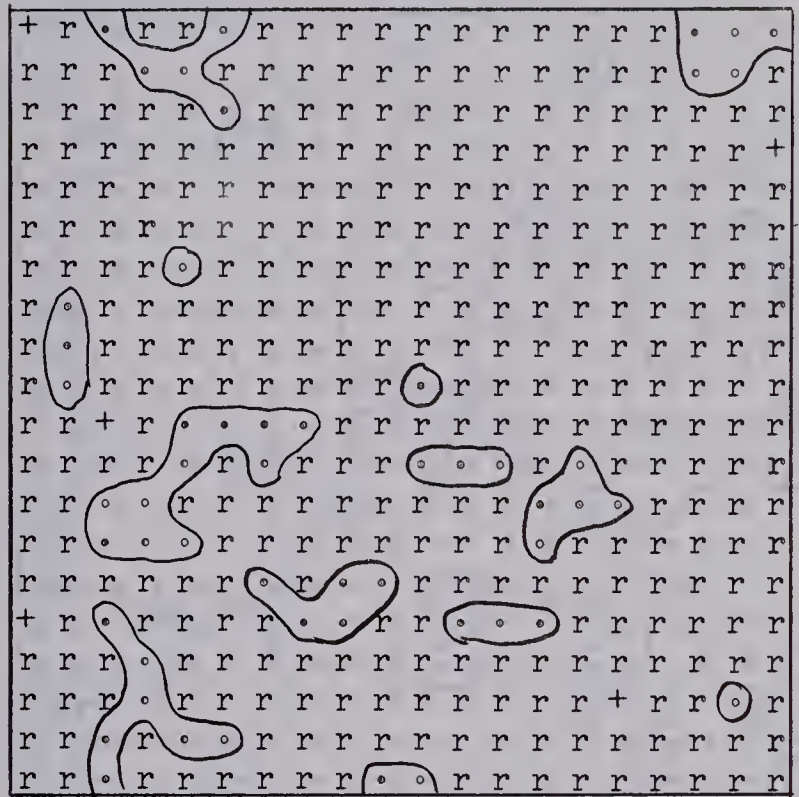


FIGURE 73

Ledum groenlandicum

47-B-I

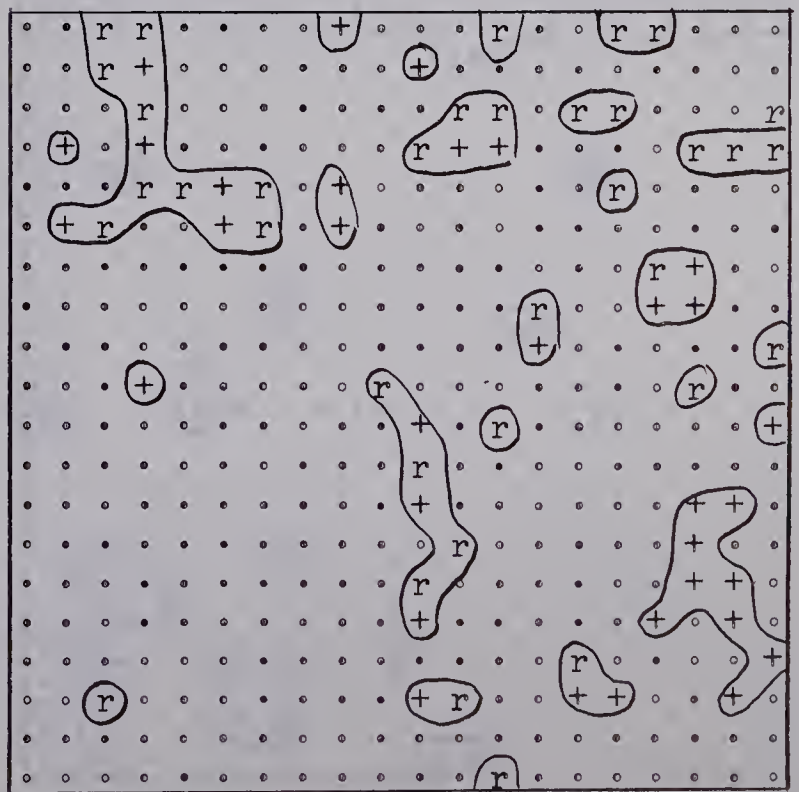




Figure 1
A network of nodes and edges
on a grid



Figure 2
A network of nodes and edges
on a grid



Figure 3
A network of nodes and edges
on a grid

FIGURE 74

Polytrichum juniperinum

47-B-I

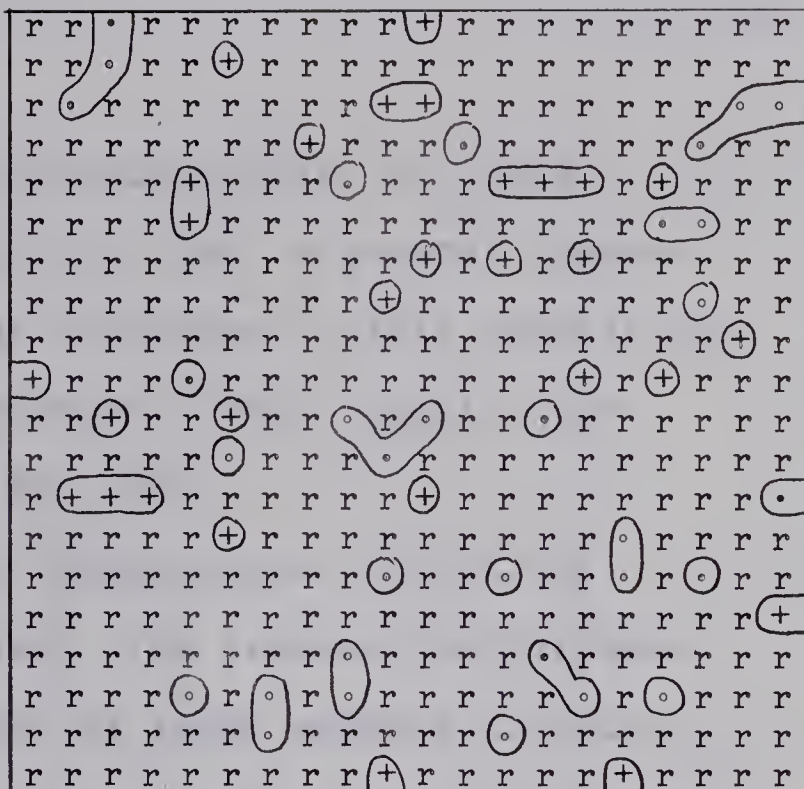


FIGURE 75

Linnaea borealis

47-B-I

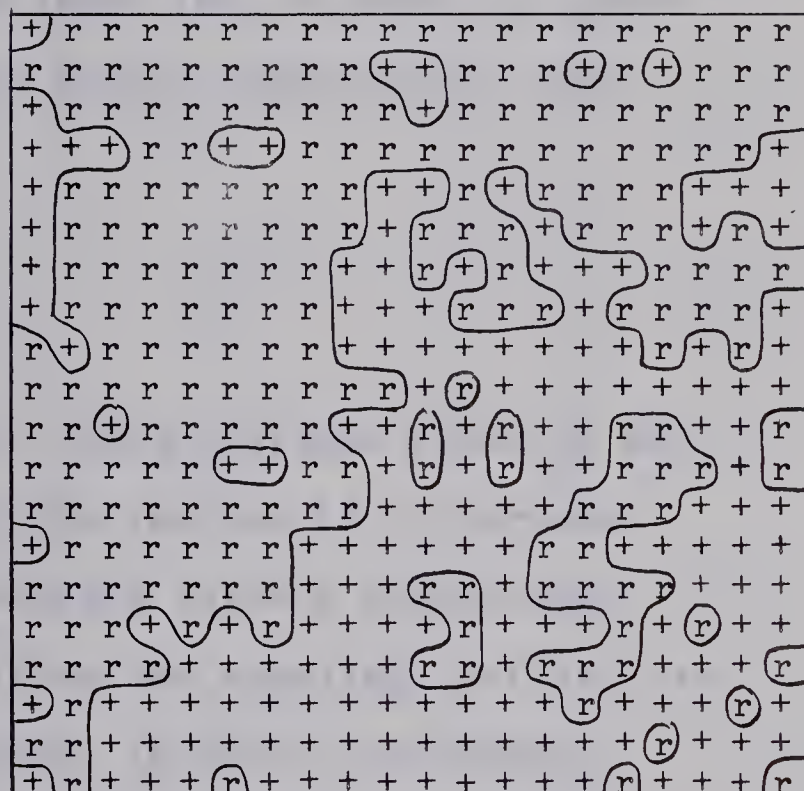
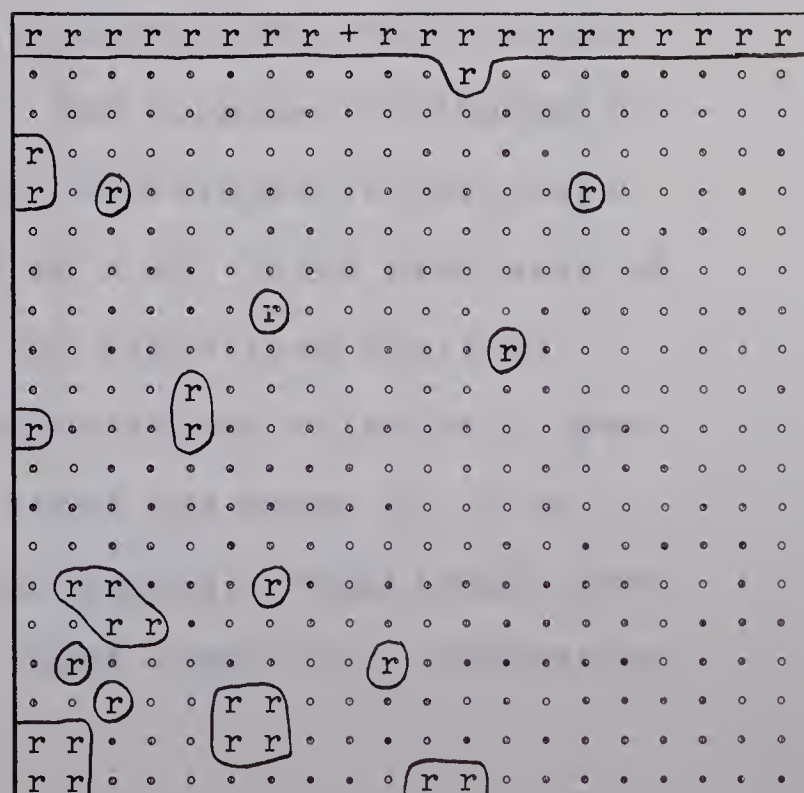


FIGURE 76

Senecio lugens

47-B-I



1. The first part of the paper is devoted to a general discussion of the problem. It is shown that the problem is of great importance for the theory of the structure of the atom. The problem is to find the wave function of the electron in the field of the nucleus. This is a difficult problem, but it is not impossible. The first step is to find the wave function of the electron in the field of the nucleus. This is a difficult problem, but it is not impossible.

2. The second part of the paper is devoted to a detailed discussion of the problem. It is shown that the problem is of great importance for the theory of the structure of the atom. The problem is to find the wave function of the electron in the field of the nucleus. This is a difficult problem, but it is not impossible. The first step is to find the wave function of the electron in the field of the nucleus. This is a difficult problem, but it is not impossible.

3. The third part of the paper is devoted to a detailed discussion of the problem. It is shown that the problem is of great importance for the theory of the structure of the atom. The problem is to find the wave function of the electron in the field of the nucleus. This is a difficult problem, but it is not impossible. The first step is to find the wave function of the electron in the field of the nucleus. This is a difficult problem, but it is not impossible.

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cordifolia (Fig. 78) *Aster ciliolatus* (Fig. 81), and *Pleurozium schreberi* (Fig. 83) all show a greater concentration of quadrats with high abundance in this depression, but quadrats with equal abundance of these species are widely scattered throughout the area.

The distribution of soil temperatures (*ca.* 15 cm) showed no recognizable pattern. The greatest differences found were due to the presence of large amounts of decaying wood in the soil. These areas tend to warm up faster during the day and also reach higher temperatures than areas of mineral soil.

3. 26-J-I: TREE STRATUM

The tree stratum of this stand contains *Picea* as did the previous two stands, but the species is *P. mariana*, not *P. engelmannii*. *Picea mariana* forms a conspicuous understory--2,800 transgressives and samplings per hectare. Forty-eight *Populus tremuloides*, 26 *Abies lasiocarpa*, 5 *Picea glauca/engelmannii* transgressives and saplings were found on the same area. The *Populus* (including 16 tree-size individuals) appears restricted to the slope joining the two terraces and to a 10 - 15 m wide area of the lower terrace adjoining the slope (see Fig. 108). The area where the *Populus* occurred was relatively open compared to the rest of the stand and rocks 2 - 4 dm in diameter protruded from the ground. Individuals from seedling to tree sizes were found (Table 14) indicating

... (1977) ...

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... (1977) ...

... (1977) ...

TABLE 14

TREE DENSITY BY SPECIES AND SIZE CLASS PER HECTARE

Numbers in brackets indicate dead individuals

| | seed- lings | trans- gres. | sap- ling | 1-3 | 3-6 | 6-9 | 9-12 | 12-15 | 15 | trees |
|----------------------------|----------------|-----------------|--------------|--------------|--------------|-------------|-----------|-------|----|---------------|
| 41-B-I | | | | | | | | | | |
| <i>Pinus contorta</i> | 28 | 6 (1) | 16 (13) | 957 (103) | 1154 (11) | 471 (15) | 6 | | | 2588 (129) |
| <i>Picea engelmannii</i> | 288 | 1653 (1) | 24 | 168 | 18 | 4 | 2 | | | 192 (1) |
| <i>Abies lasiocarpa</i> | 129 | 479 | 28 | 37 | 11 | 2 | | | | 50 |
| TOTALS | 445 | 2138 | 68 | 1162 | 1183 | 477 | 8 | | | 2830 (412) |
| 47-B-I | | | | | | | | | | |
| <i>Pinus contorta</i> | 114 (1) | 2 | 19 (171) | 441 (818) | 2900 (94) | 303 (1) | 3 | | | 3647 (913) |
| <i>Picea engelmannii</i> | 107 | | 438 | 173 (3) | 80 | | | | | 253 (3) |
| <i>Abies lasiocarpa</i> | 40 | | 27 | 1 | | | | | | 1 |
| <i>Populus tremuloides</i> | | | 3 | | | | | | | |
| TOTALS | 261 | 2 | 487 | 515 | 2980 | 303 | 3 | | | 3801 (916) |
| 26-J-I | | | | | | | | | | |
| <i>Pinus contorta</i> | 374 | 281 (3) | 35 (6) | 225 (191) | 542 (147) | 136 (56) | 28 (5) | | | 966 (399) |
| <i>Picea mariana</i> | 153 | 2768 | 48 | 90 (6) | 115 (4) | 35 (1) | | | | 240 (13) |
| <i>Populus tremuloides</i> | 25 | 21 | 2 | | 8 | 8 | 1 | | | 17 |
| <i>Abies lasiocarpa</i> | 6 | 24 (1) | 2 | | | | | | | |

| Date | | Page | | No. | |
|------|--|------|--|-----|--|
| 1900 | | 1 | | 1 | |
| 1901 | | 2 | | 2 | |
| 1902 | | 3 | | 3 | |
| 1903 | | 4 | | 4 | |
| 1904 | | 5 | | 5 | |
| 1905 | | 6 | | 6 | |
| 1906 | | 7 | | 7 | |
| 1907 | | 8 | | 8 | |
| 1908 | | 9 | | 9 | |
| 1909 | | 10 | | 10 | |
| 1910 | | 11 | | 11 | |
| 1911 | | 12 | | 12 | |
| 1912 | | 13 | | 13 | |
| 1913 | | 14 | | 14 | |
| 1914 | | 15 | | 15 | |
| 1915 | | 16 | | 16 | |
| 1916 | | 17 | | 17 | |
| 1917 | | 18 | | 18 | |
| 1918 | | 19 | | 19 | |
| 1919 | | 20 | | 20 | |
| 1920 | | 21 | | 21 | |
| 1921 | | 22 | | 22 | |
| 1922 | | 23 | | 23 | |
| 1923 | | 24 | | 24 | |
| 1924 | | 25 | | 25 | |
| 1925 | | 26 | | 26 | |
| 1926 | | 27 | | 27 | |
| 1927 | | 28 | | 28 | |
| 1928 | | 29 | | 29 | |
| 1929 | | 30 | | 30 | |
| 1930 | | 31 | | 31 | |
| 1931 | | 32 | | 32 | |
| 1932 | | 33 | | 33 | |
| 1933 | | 34 | | 34 | |
| 1934 | | 35 | | 35 | |
| 1935 | | 36 | | 36 | |
| 1936 | | 37 | | 37 | |
| 1937 | | 38 | | 38 | |
| 1938 | | 39 | | 39 | |
| 1939 | | 40 | | 40 | |
| 1940 | | 41 | | 41 | |
| 1941 | | 42 | | 42 | |
| 1942 | | 43 | | 43 | |
| 1943 | | 44 | | 44 | |
| 1944 | | 45 | | 45 | |
| 1945 | | 46 | | 46 | |
| 1946 | | 47 | | 47 | |
| 1947 | | 48 | | 48 | |
| 1948 | | 49 | | 49 | |
| 1949 | | 50 | | 50 | |
| 1950 | | 51 | | 51 | |
| 1951 | | 52 | | 52 | |
| 1952 | | 53 | | 53 | |
| 1953 | | 54 | | 54 | |
| 1954 | | 55 | | 55 | |
| 1955 | | 56 | | 56 | |
| 1956 | | 57 | | 57 | |
| 1957 | | 58 | | 58 | |
| 1958 | | 59 | | 59 | |
| 1959 | | 60 | | 60 | |
| 1960 | | 61 | | 61 | |
| 1961 | | 62 | | 62 | |
| 1962 | | 63 | | 63 | |
| 1963 | | 64 | | 64 | |
| 1964 | | 65 | | 65 | |
| 1965 | | 66 | | 66 | |
| 1966 | | 67 | | 67 | |
| 1967 | | 68 | | 68 | |
| 1968 | | 69 | | 69 | |
| 1969 | | 70 | | 70 | |
| 1970 | | 71 | | 71 | |
| 1971 | | 72 | | 72 | |
| 1972 | | 73 | | 73 | |
| 1973 | | 74 | | 74 | |
| 1974 | | 75 | | 75 | |
| 1975 | | 76 | | 76 | |
| 1976 | | 77 | | 77 | |
| 1977 | | 78 | | 78 | |
| 1978 | | 79 | | 79 | |
| 1979 | | 80 | | 80 | |
| 1980 | | 81 | | 81 | |
| 1981 | | 82 | | 82 | |
| 1982 | | 83 | | 83 | |
| 1983 | | 84 | | 84 | |
| 1984 | | 85 | | 85 | |
| 1985 | | 86 | | 86 | |
| 1986 | | 87 | | 87 | |
| 1987 | | 88 | | 88 | |
| 1988 | | 89 | | 89 | |
| 1989 | | 90 | | 90 | |
| 1990 | | 91 | | 91 | |
| 1991 | | 92 | | 92 | |
| 1992 | | 93 | | 93 | |
| 1993 | | 94 | | 94 | |
| 1994 | | 95 | | 95 | |
| 1995 | | 96 | | 96 | |
| 1996 | | 97 | | 97 | |
| 1997 | | 98 | | 98 | |
| 1998 | | 99 | | 99 | |
| 1999 | | 100 | | 100 | |

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 0-13-000000-0

TABLE 14 Cont'd.

| | seed- lings | trans- gres. | sap- ling | 1-3 | 3-6 | 6-9 | 9-12 | 12-15 | 15 | trees |
|---------------------------------|----------------|-----------------------|--------------------|--------------------|-------------------|------------------|------------|----------------|----|----------------|
| <i>Picea glauca/engelmannii</i> | 2 | 3 | | 4 | | | | | | 4 |
| TOTALS | 560 | 3097 (4) | 59 (6) | 129 (197) | 348 (151) | 585 (57) | 137 (7) | 28 | | 1227 (412) |
| <hr/> | | | | | | | | | | |
| 55-J-I | | | | | | | | | | |
| <i>Pinus contorta</i> | 3353 3353 | 2615 2615 (157) | 301 301 (30) | 128 301 (30) | 197 128 (4) | 96 197 (1) | 34 96 | 3 34 (1) | 3 | 759 (36) |
| <i>Picea glauca</i> | 6 | 3 | 1 | | | | | | | |
| <i>Abies lasiocarpa</i> | 8 | | | | | | | | | |
| <i>Populus tremuloides</i> | 21 | 17 (1) | 7 | | | | | | | |
| TOTALS | 3368 | 2643 (158) | 301 (30) | 128 (4) | 197 (1) | 96 | 34 (1) | 3 | | (36) |
| <hr/> | | | | | | | | | | |
| 24-J-I | | | | | | | | | | |
| <i>Pinus contorta</i> | 384 (1) | 223 (224) | 197 (774) | 1946 (1184) | 658 (9) | 94 (1) | 48 (2) | 18 | | 2764 (1197) |
| <i>Picea mariana</i> | | 7 | | | 2 | | | | | 4 |
| <i>Picea glauca</i> | 25 | 2 | 3 | | | 1 | | | | 1 |
| <i>Abies lasiocarpa</i> | 7 | | 1 | | | | | | | |
| TOTALS | 412 (1) | 232 (224) | 204 (774) | 1948 (1185) | 660 (9) | 95 (1) | 48 (2) | 18 | | 2769 (1197) |

FIGURE 77

Elymus innovatus

47-B-I

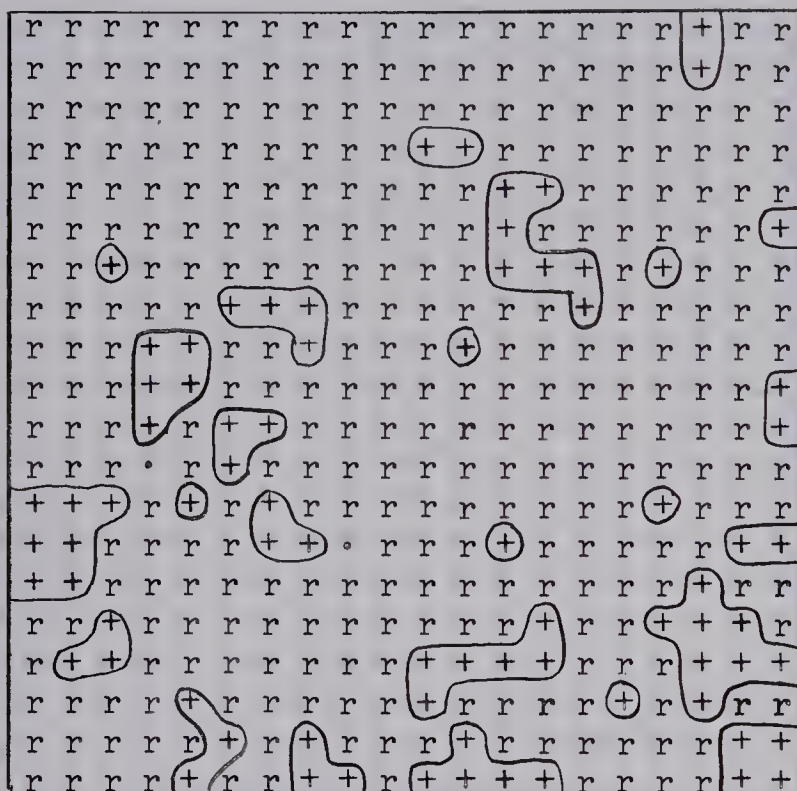


FIGURE 78

Arnica cordifolia

47-B-I

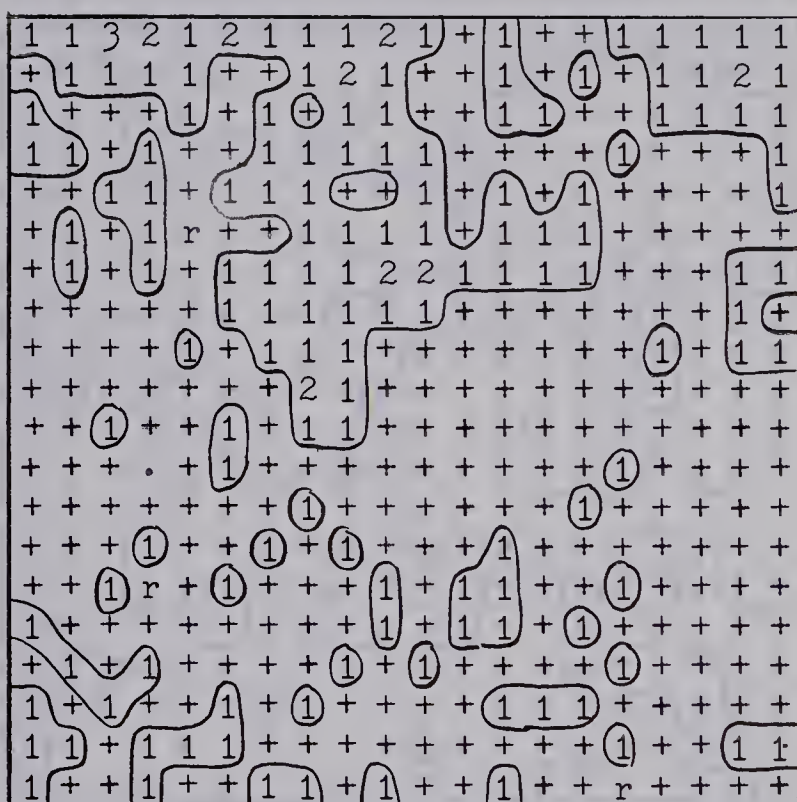


FIGURE 79

Cornus canadensis

47-B-I

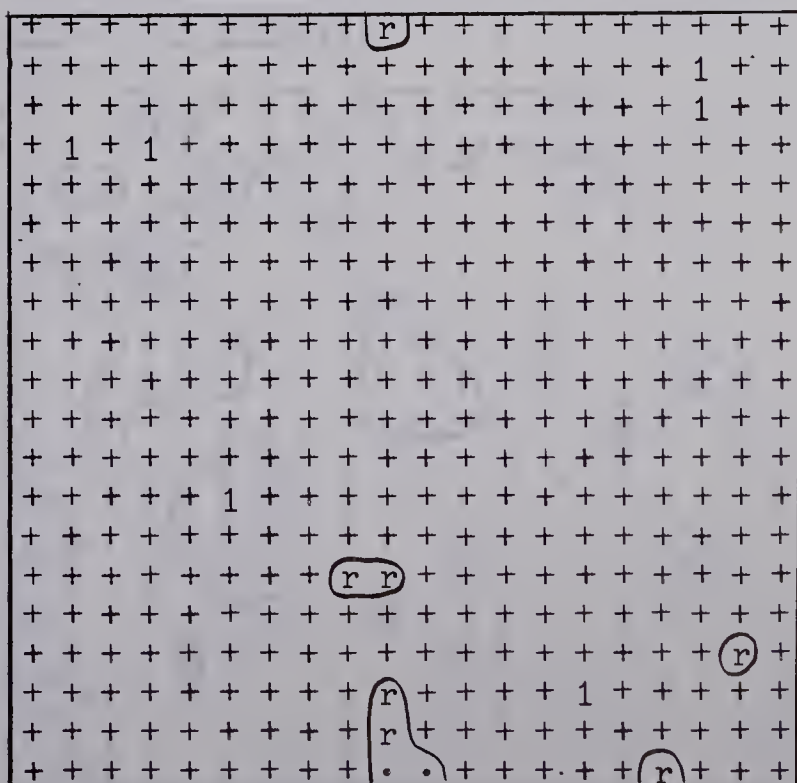


FIGURE 80

Epilobium angustifolium

47-B-I

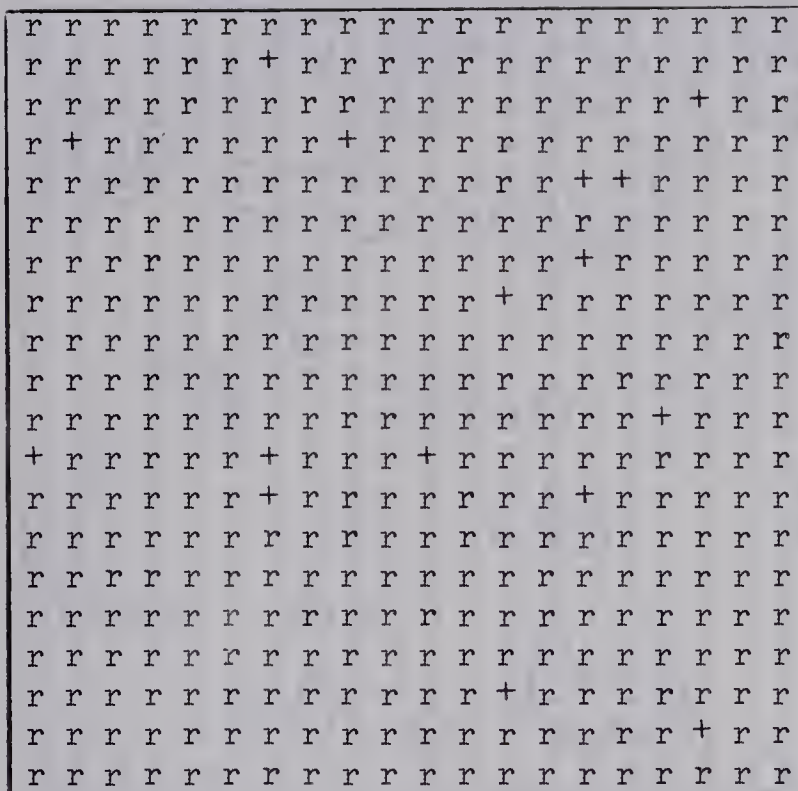


FIGURE 81

Aster ciliolatus

47-B-I

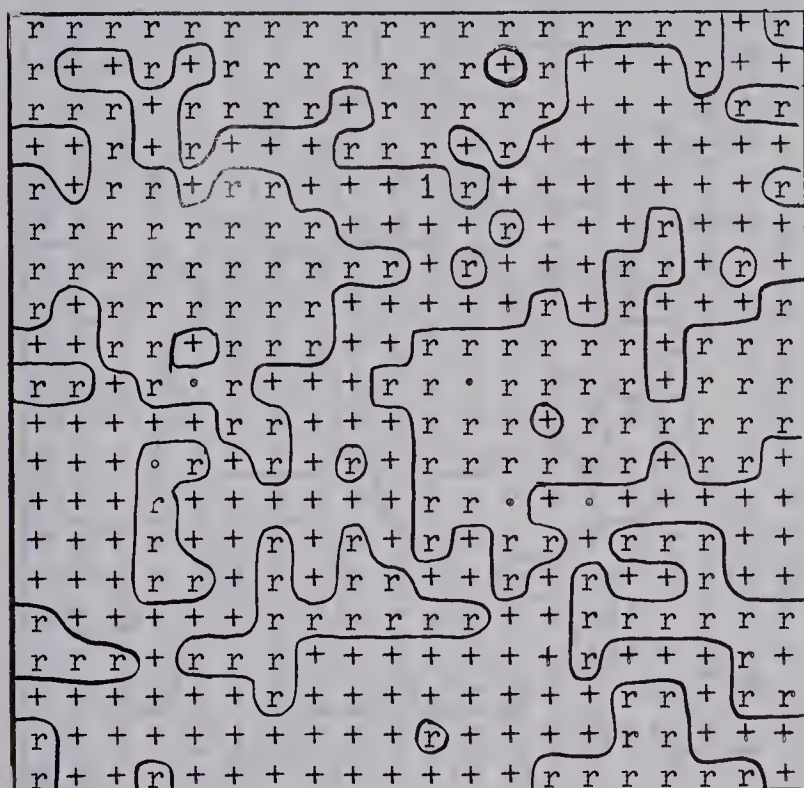


FIGURE 82

Aster conspicuus

47-B-I

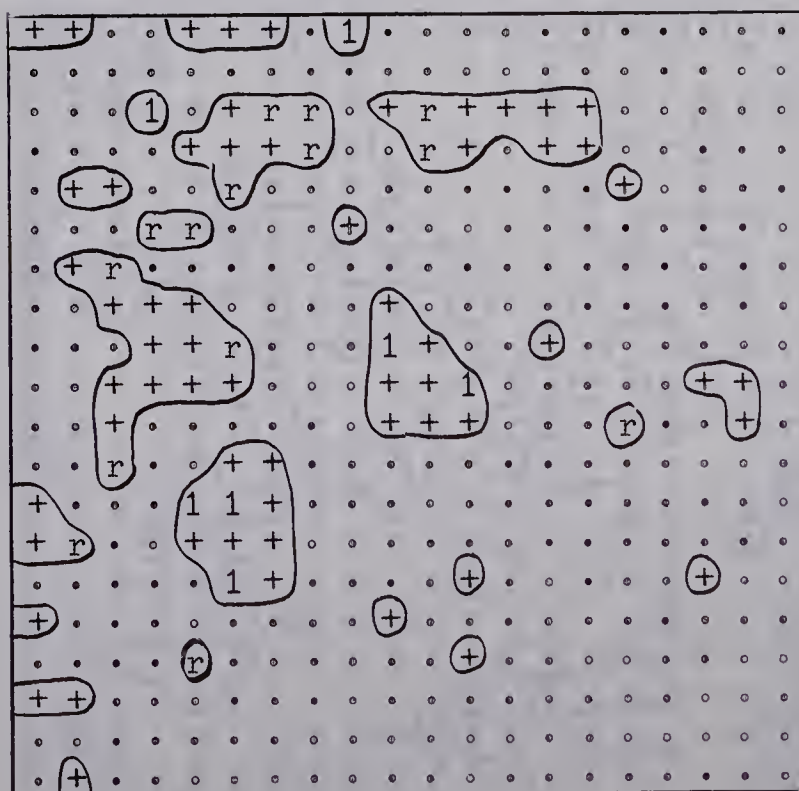


FIGURE 83

Pleurozium schreberi

47-B-I

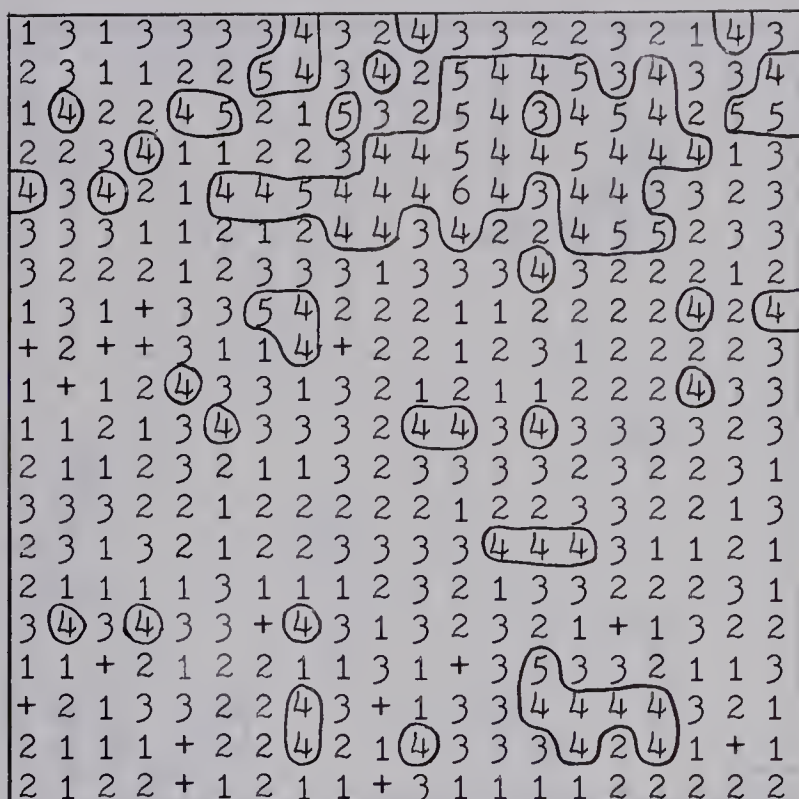


FIGURE 84

Ptilium crista-castrensis

47-B-I

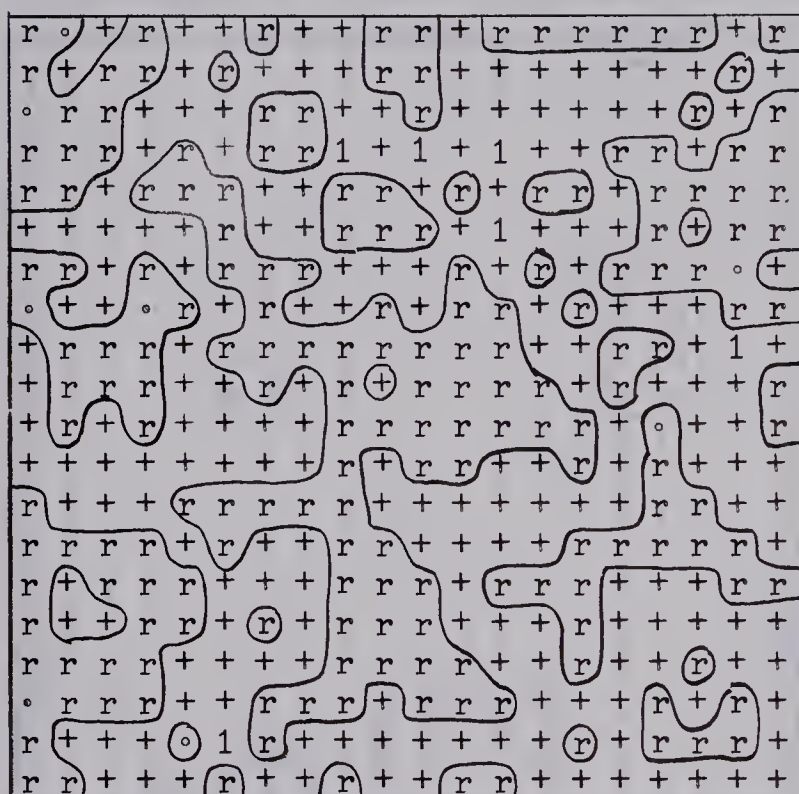
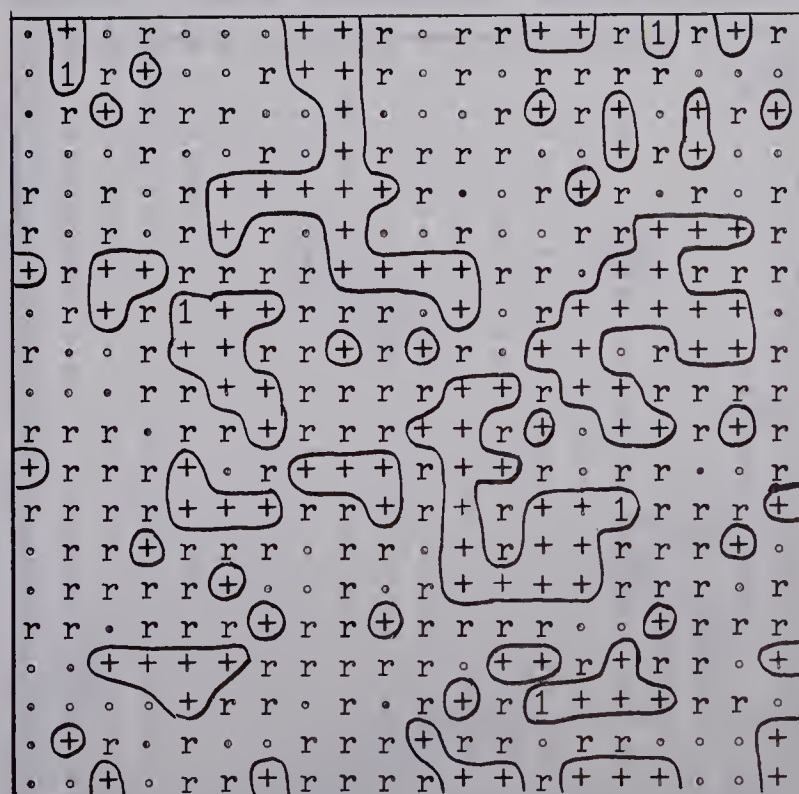


FIGURE 85

Hylocomium splendens

47-B-I





NO. 10000
 (Handwritten number)
 10000



NO. 10001
 (Handwritten number)
 10001



NO. 10002
 (Handwritten number)
 10002



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BUREAU OF LAND MANAGEMENT
WASHINGTON, D. C. 20240

FIGURE 89

Rhododendron albiflorum

47-B-I

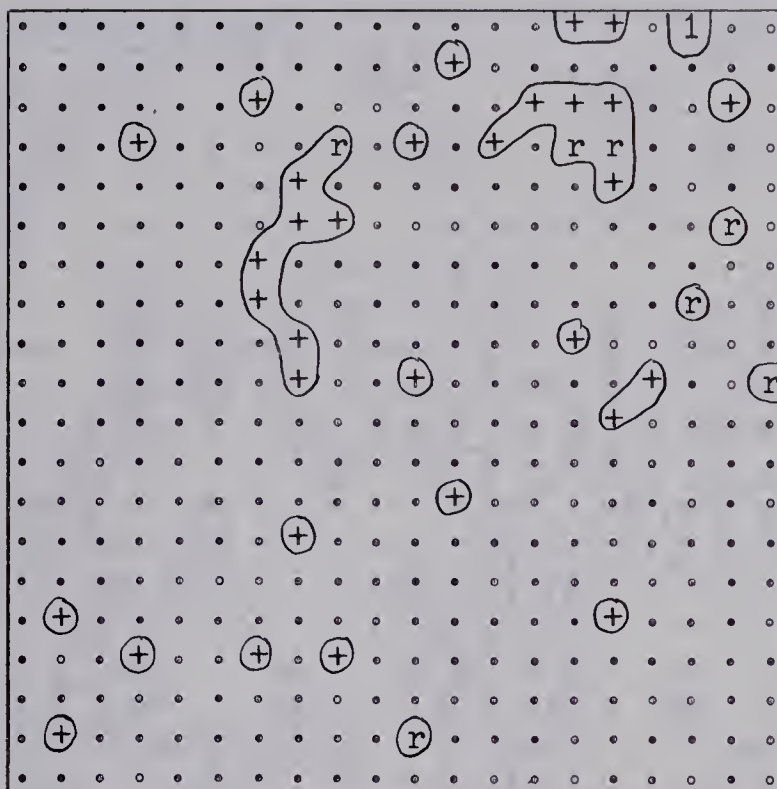


FIGURE 90

Phyllodoce spp.

47-B-I

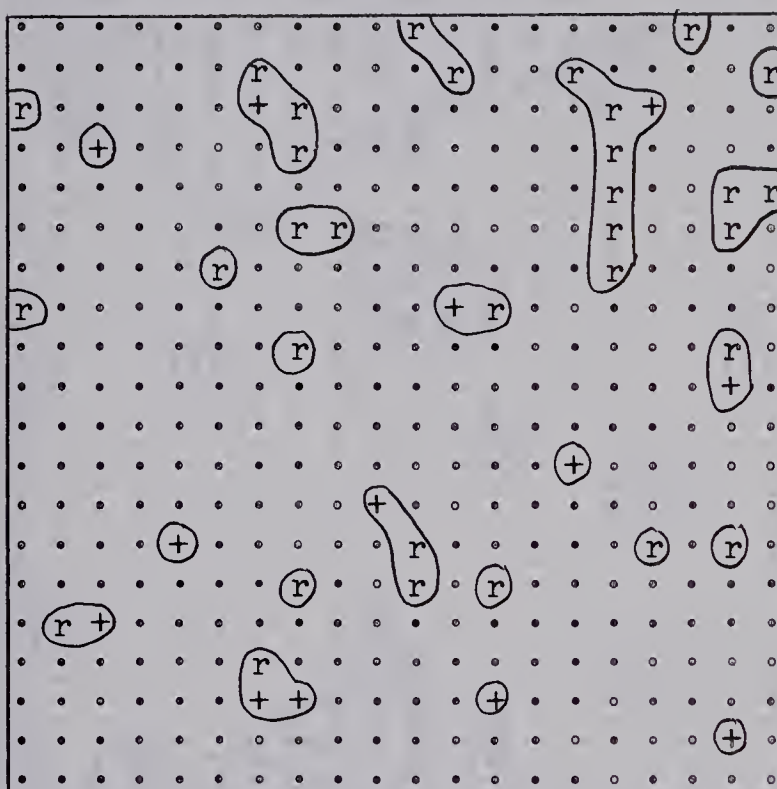
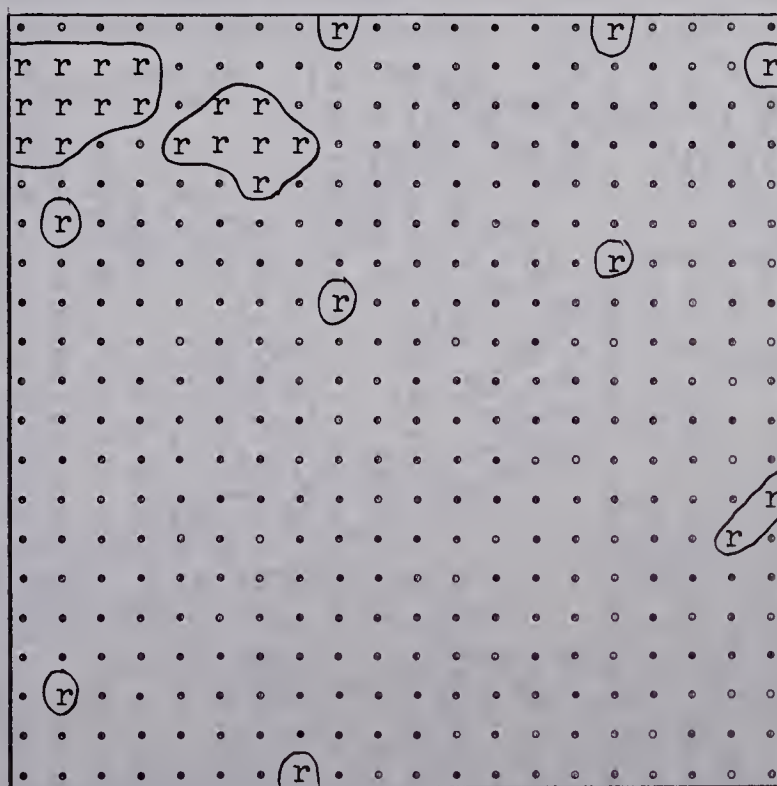


FIGURE 91

Stenanthium occidentale

47-B-I





10-0000
 10-0000
 10-0000



10-0000
 10-0000
 10-0000



10-0000
 10-0000
 10-0000

FIGURE 92

Juniperus communis

47-B-I

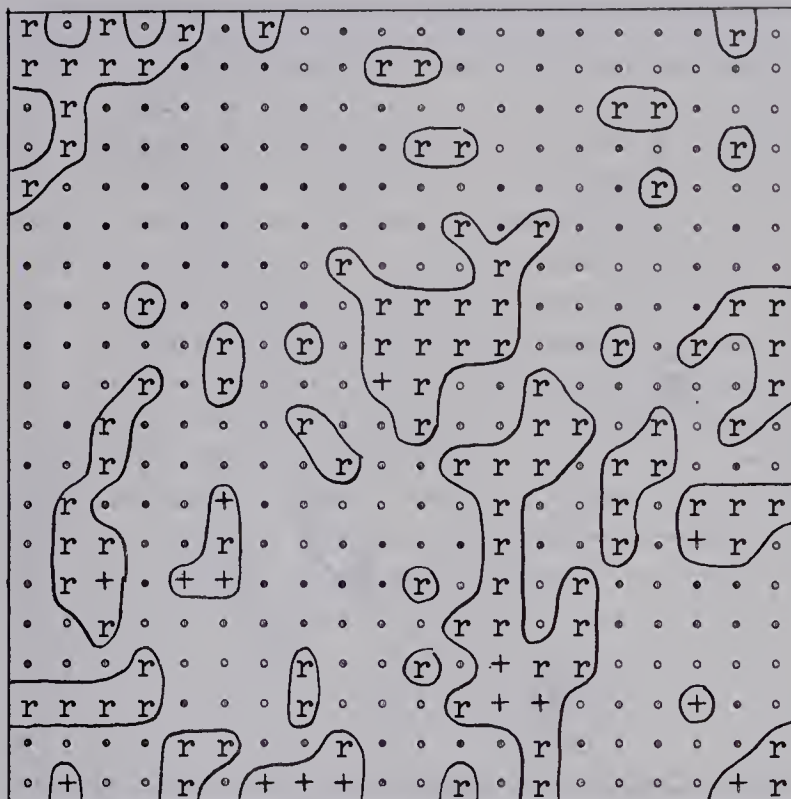


FIGURE 93

Calamagrostis sp.

47-B-I

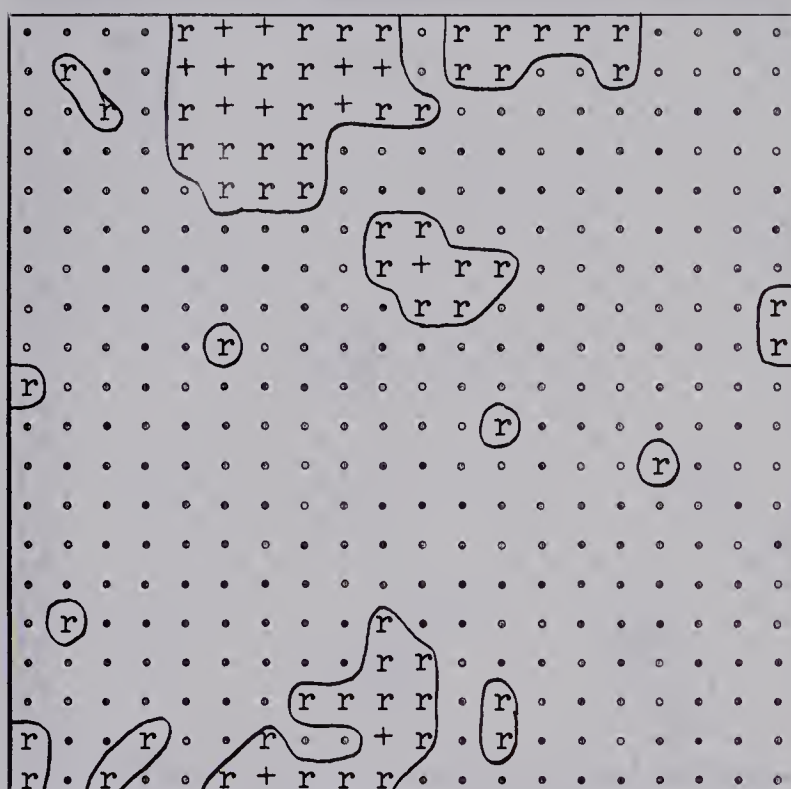


FIGURE 94

Salix spp.

47-B-I

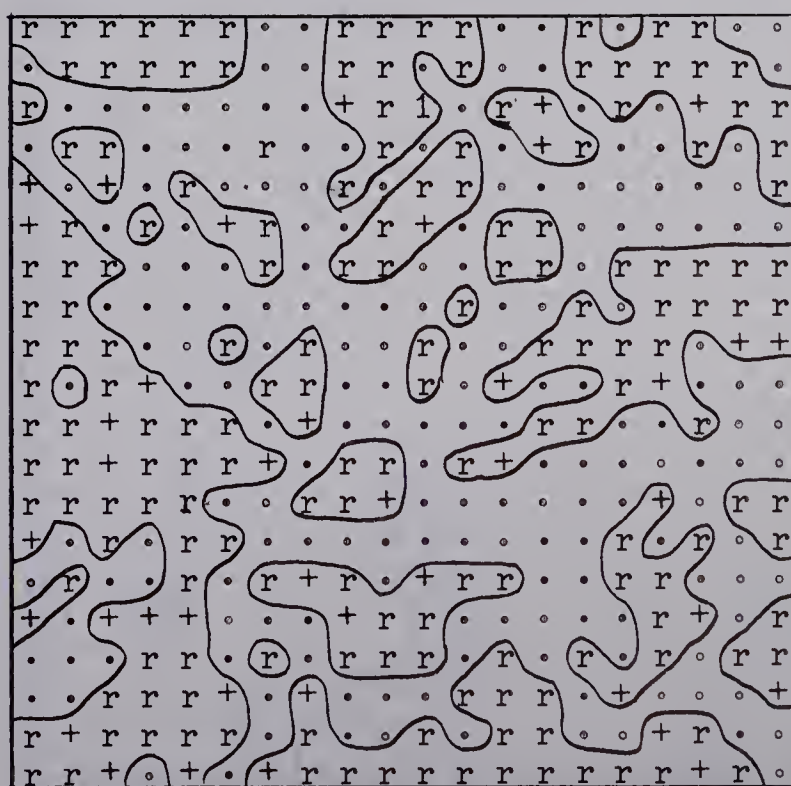


FIGURE 95

Calypso bulbosa

47-B-I

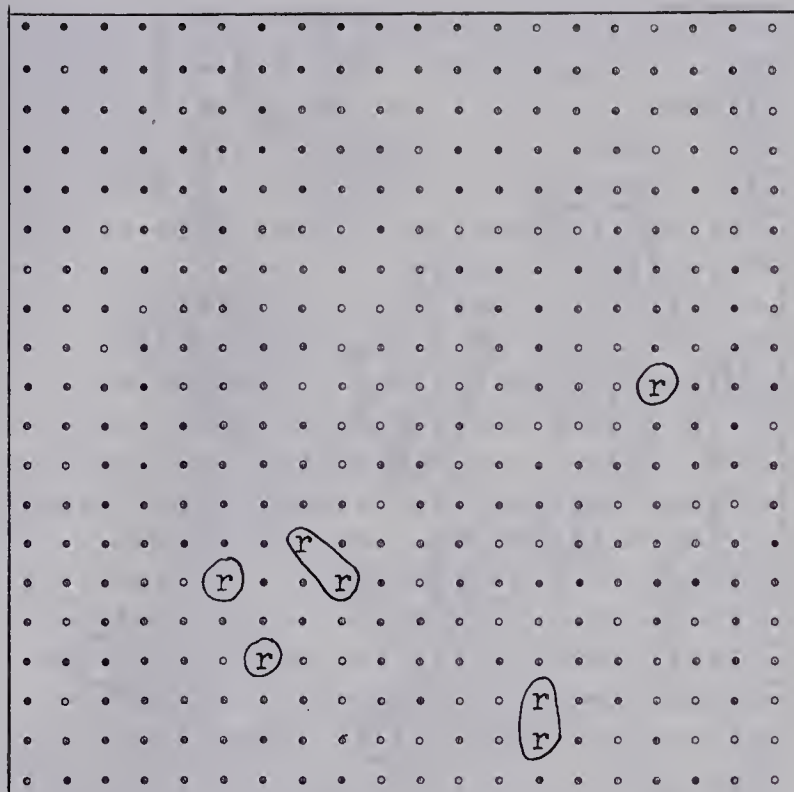


FIGURE 96

Solidago multiradiata

47-B-I

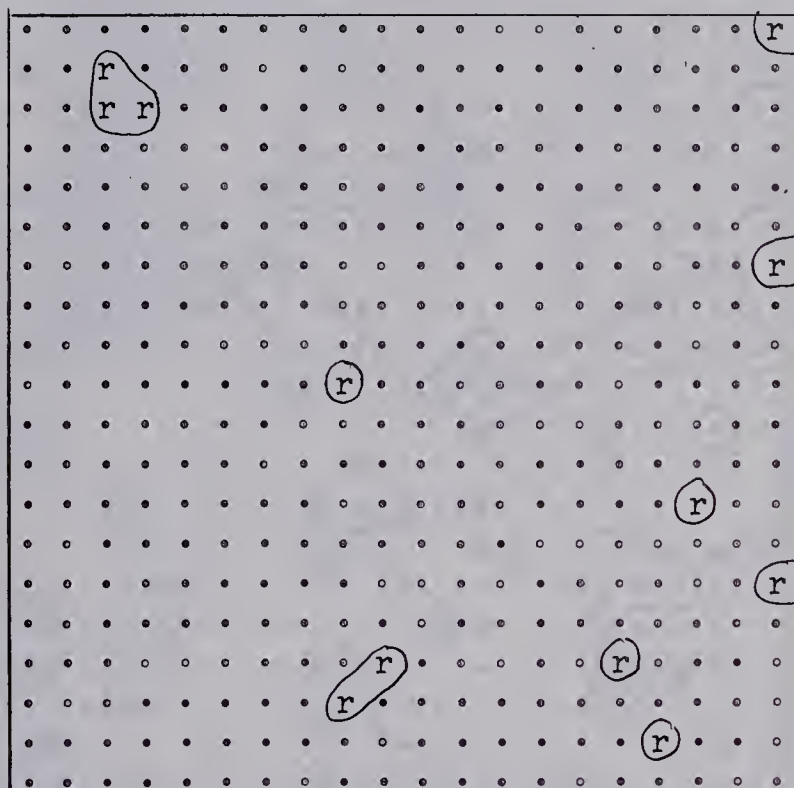
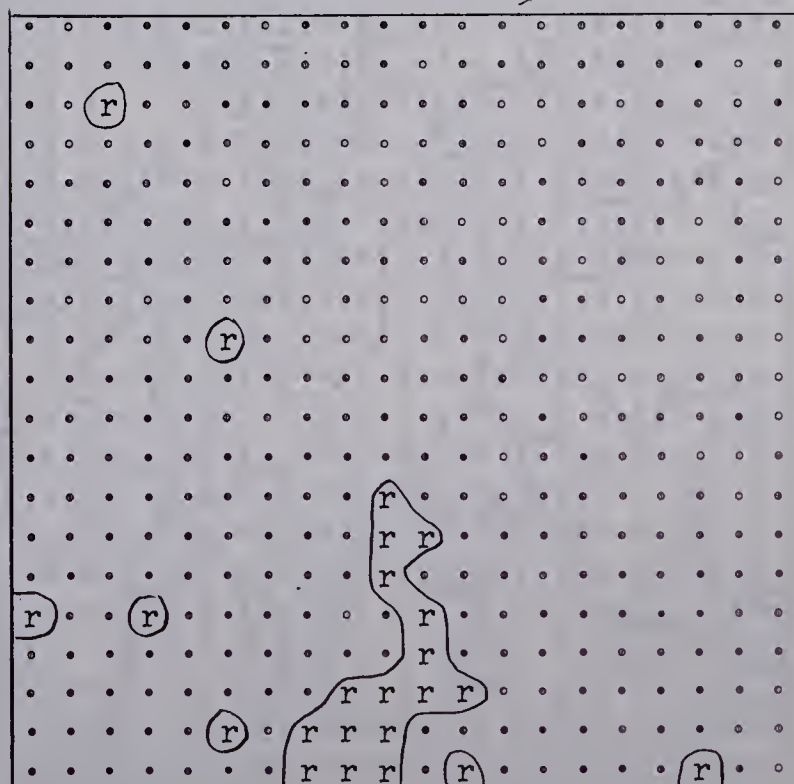
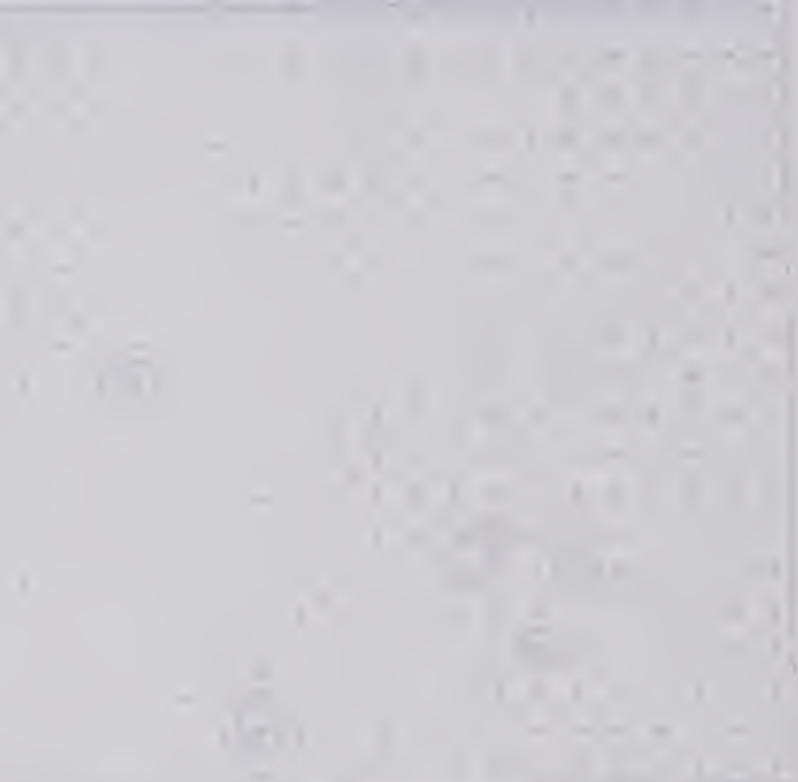


FIGURE 97

Castilleja miniata

47-B-I





NO. 100000
 Length 100000
 100000



NO. 100000
 Length 100000
 100000



NO. 100000
 Length 100000
 100000

FIGURE 98

Shepherdia canadensis

47-B-I

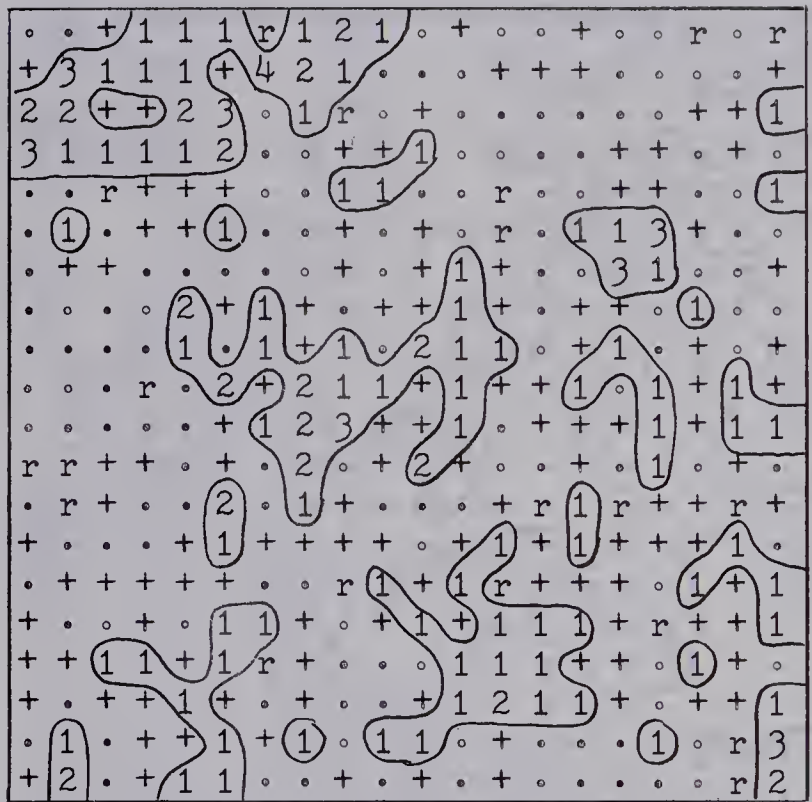


FIGURE 99

Menziesia glabella

47-B-I

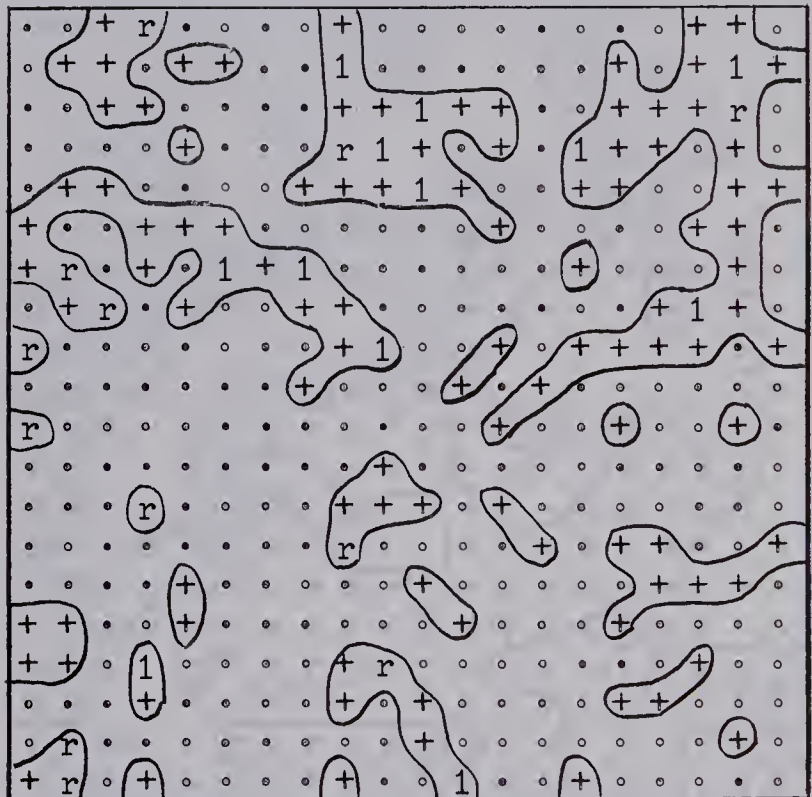
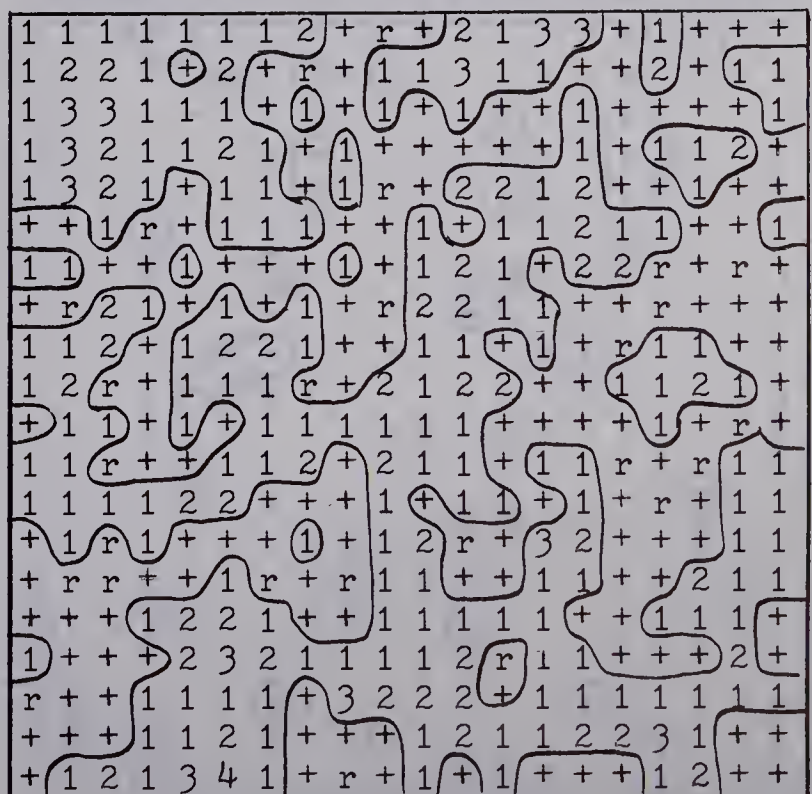


FIGURE 100

Vaccinium scoparium

47-B-I





AT 20011
Commersonia diffusa
 (L.)



AT 20012
Commersonia diffusa
 (L.)



AT 20013
Commersonia diffusa
 (L.)

FIGURE 101

Pyrola secunda

47-B-I

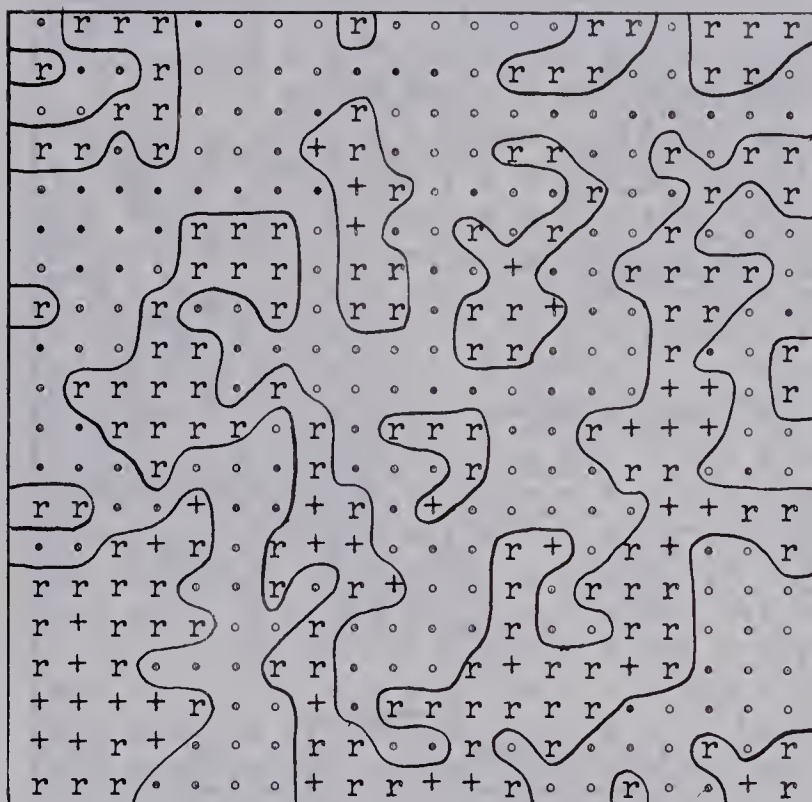


FIGURE 102

Pyrola virens

47-B-I

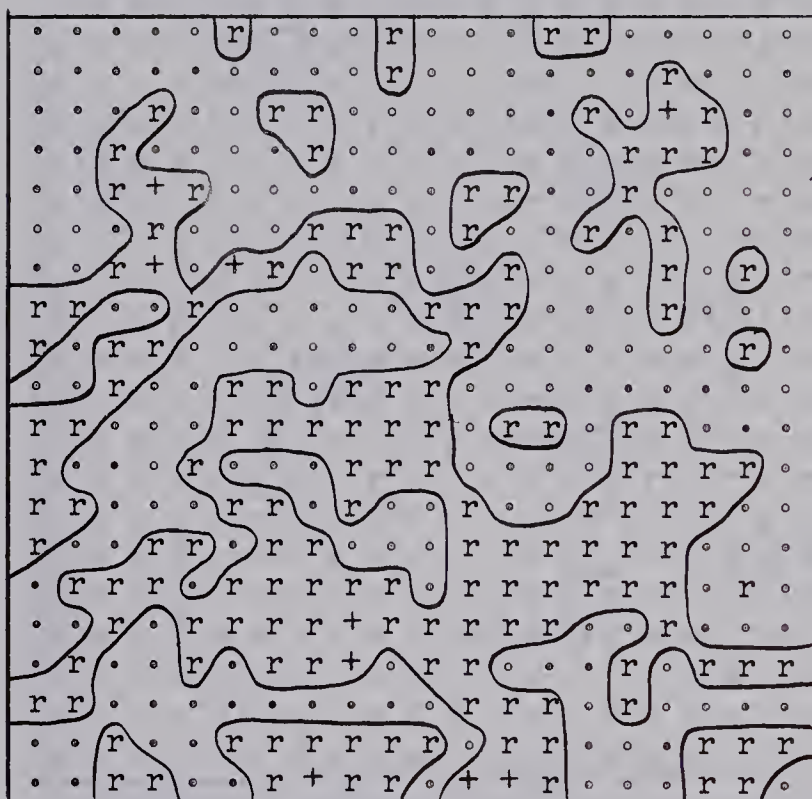


FIGURE 103

Chimaphila umbellata

47-B-I

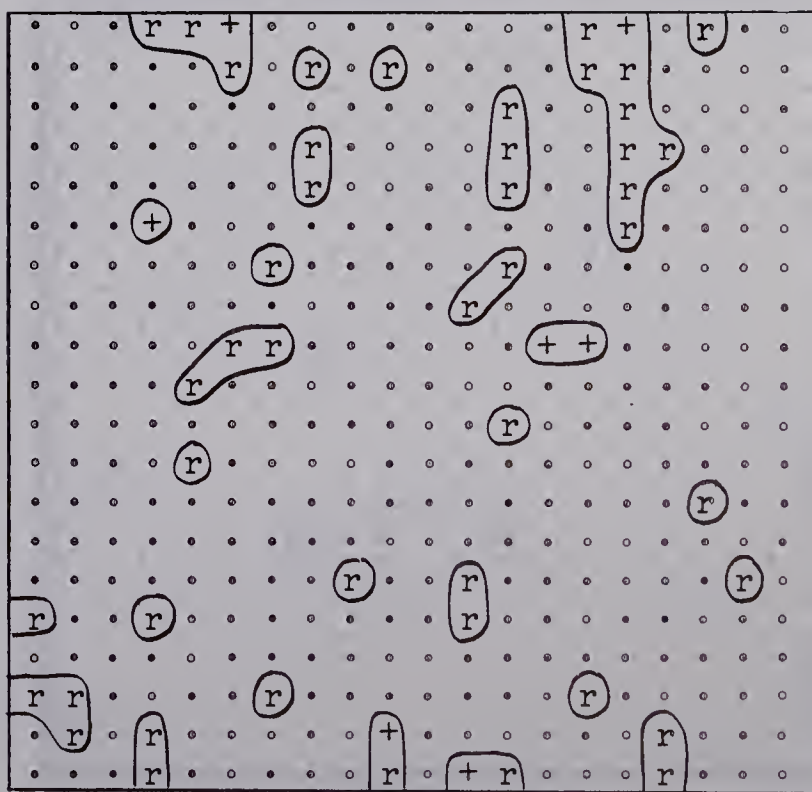


FIGURE 104

Dicranum polysetum

47-B-I

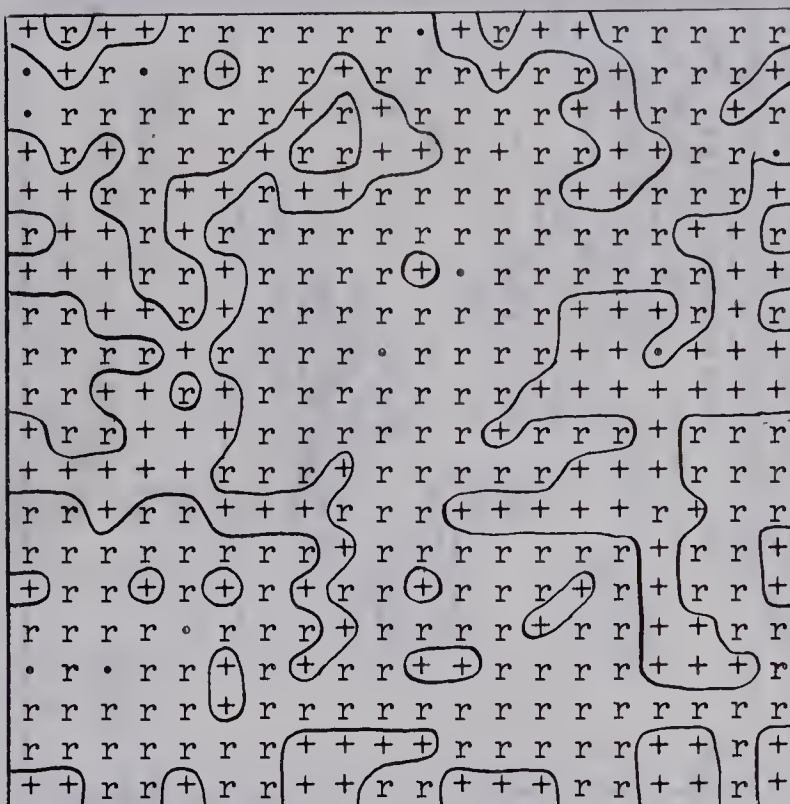


FIGURE 105

Carex spp.

47-B-I

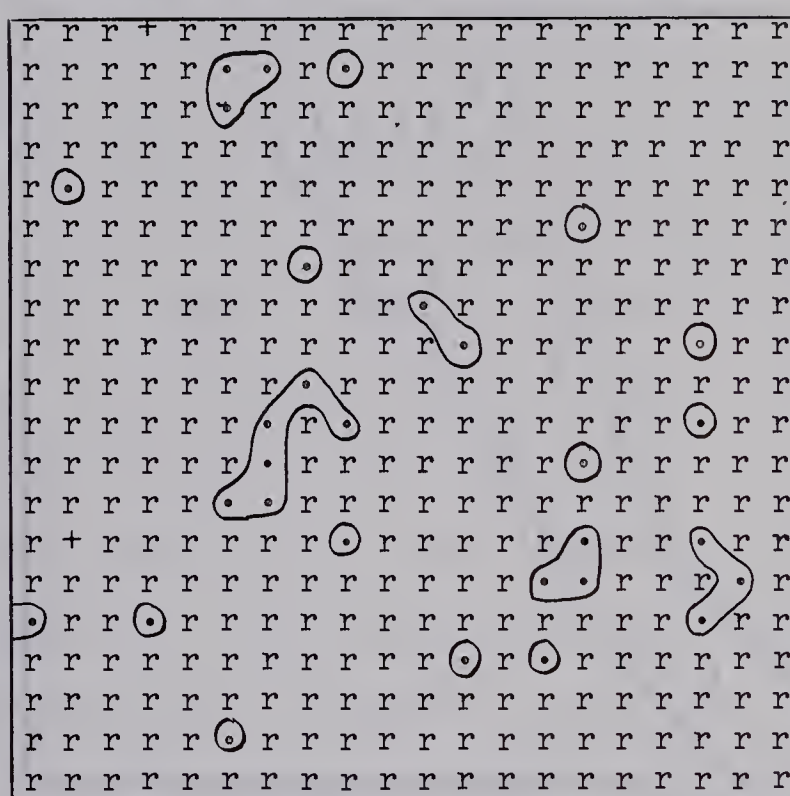
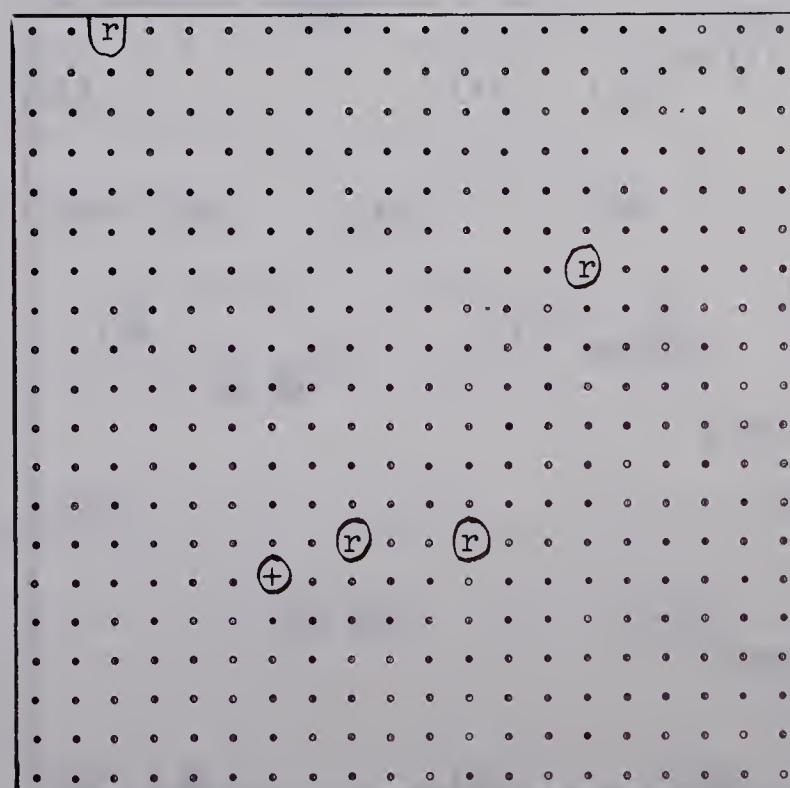


FIGURE 106

Moneses uniflora

47-B-I





1000 1000
1000 1000
1000 1000



1000 1000
1000 1000
1000 1000



1000 1000
1000 1000
1000 1000

FIGURE 107

26-J-I

Picea mariana

trees

1= 1 individual

2= 2 individuals

3= 3-6 individuals.

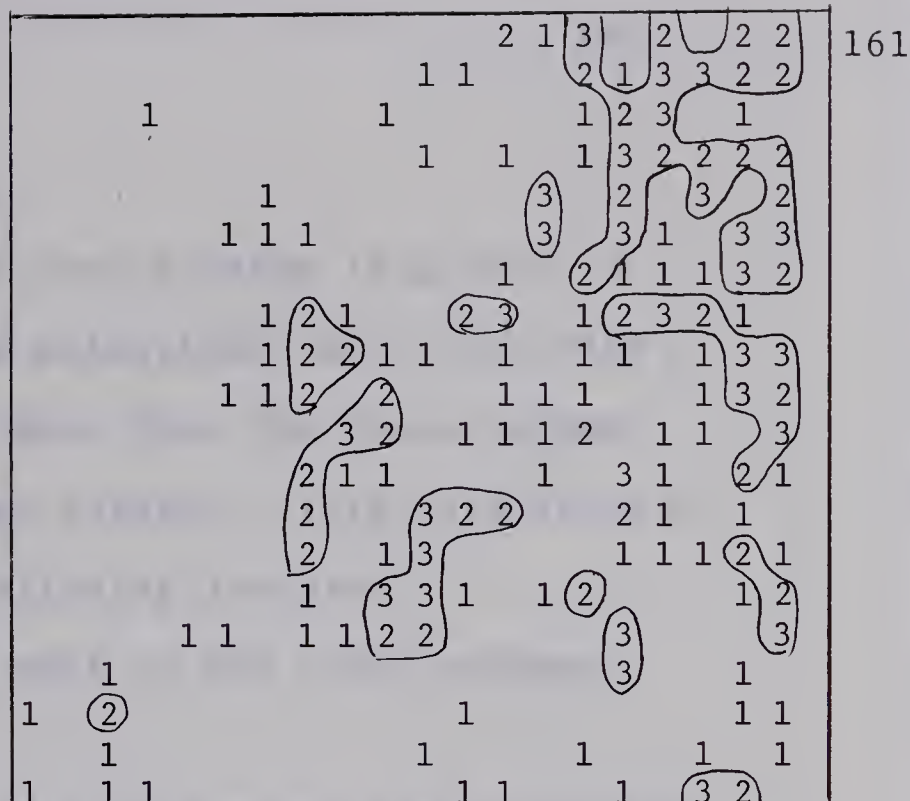


FIGURE 108

26-J-I

Populus tremuloides

trees

numbers = actual

numbers of individuals

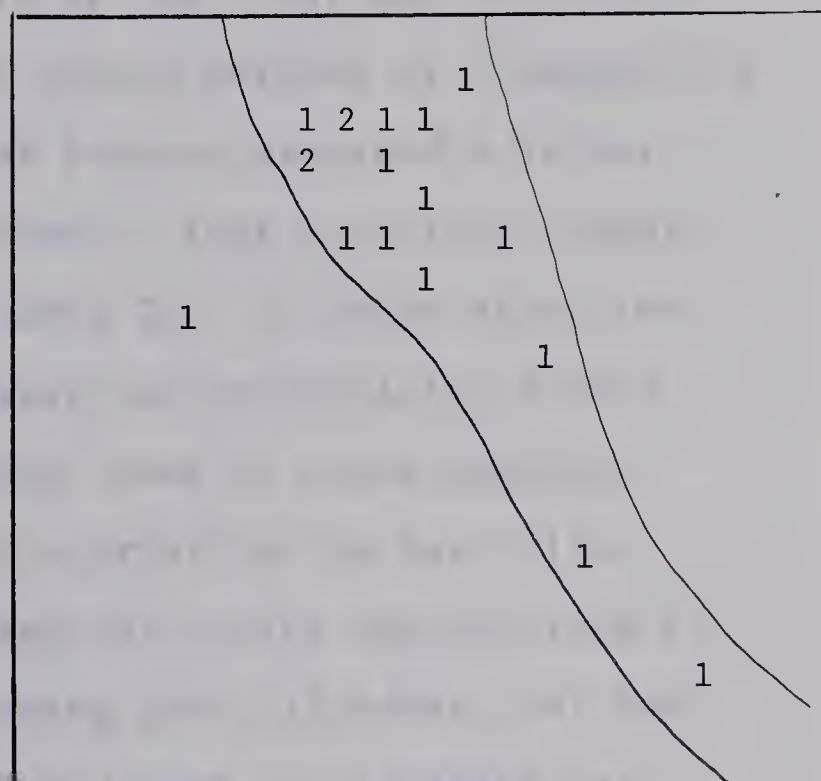


FIGURE 109

26-J-I

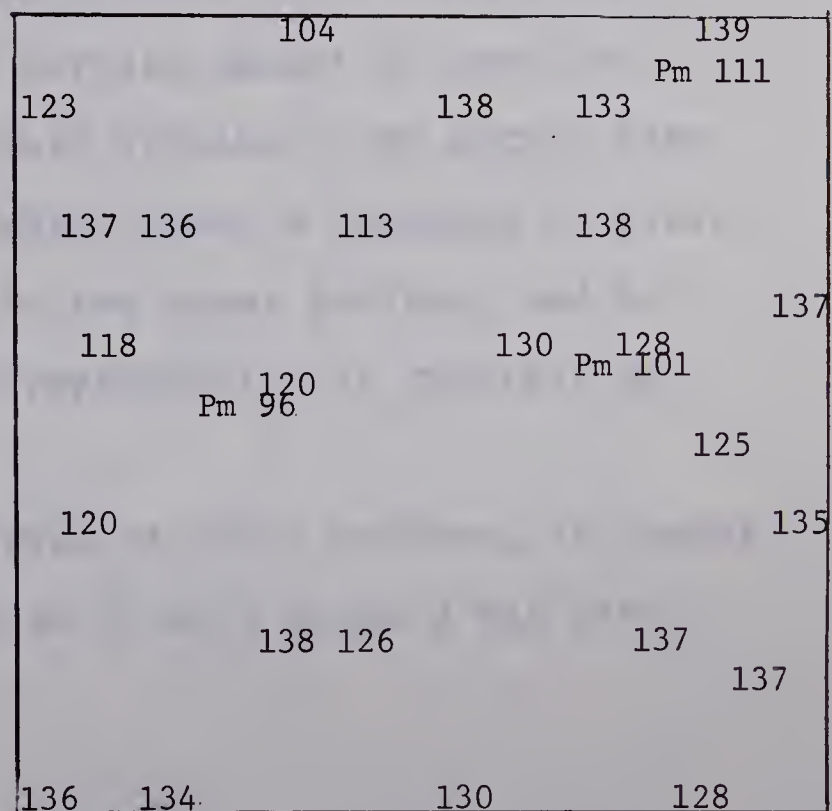
tree ages

unlabelled numbers

refer to *Pinus contorta*

Pm refers to

Picea mariana



a locally favourable habitat.

From the age data of the tree stratum (Fig.109) it appears that the *Picea* became established after the pine. From Fig.107 and 110 it is evident that the *Picea* became established first on the lower terrace. This distribution could be due to any of the following factors:

1. seed trees in areas next to the river escaped the last fire, or
2. seeds were brought in by the river and deposited on the lower terrace during periods of flooding, or
3. the lower and moister terrace provided a better "seed bed" for the *Picea*. That the *Picea* appears to have invaded the area 20 - 30 years after the pine, tends to diminish the probability of seed coming from serotinous cones of *Picea mariana* which were on the site prior to the last fire.

Picea is actively invading this site; reproduction is abundant, primarily from layering from old trees, but the presence of young plants isolated from any layering individuals must indicate that a certain amount of seed is germinating and surviving. This hypothesis of active invasion is supported by Fig.107 which shows a decrease in *Picea* tree density from the lower to the upper terrace, and by Fig.110 which indicates that reproduction is greatest on the lower terrace.

Despite the active invasion of *Picea mariana*, it cannot be unequivocally concluded that it will succeed the pine.

FIGURE 110

26-J-I

Picea mariana

transgressives

1= 1-9 individuals

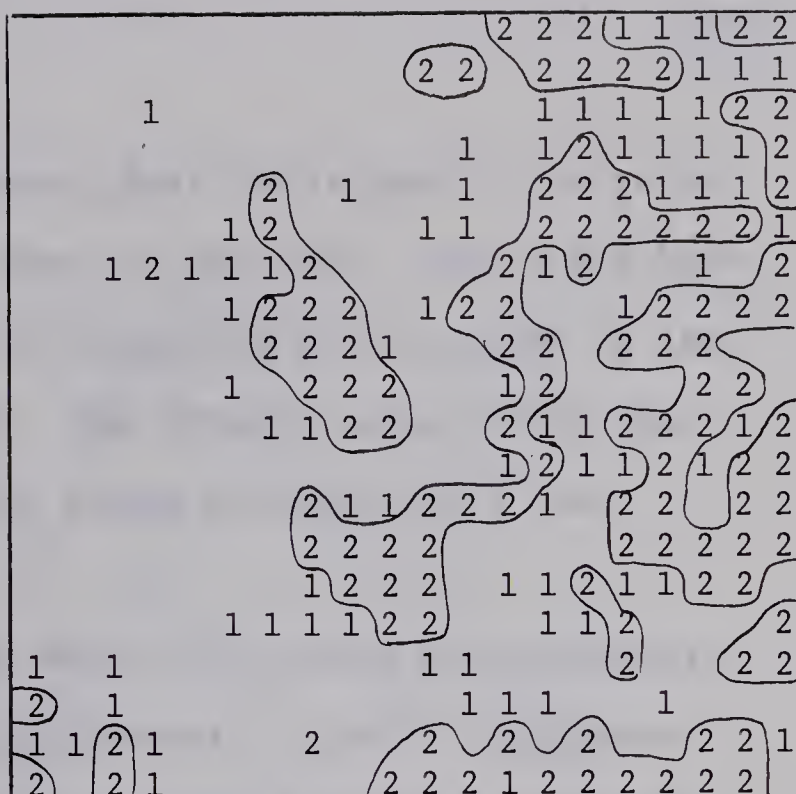
2= more than 9
individuals

FIGURE 111

26-J-I

Pinus contorta

trees

1= 1 individual

2= 2-3 individuals

3= 4-8 individuals.

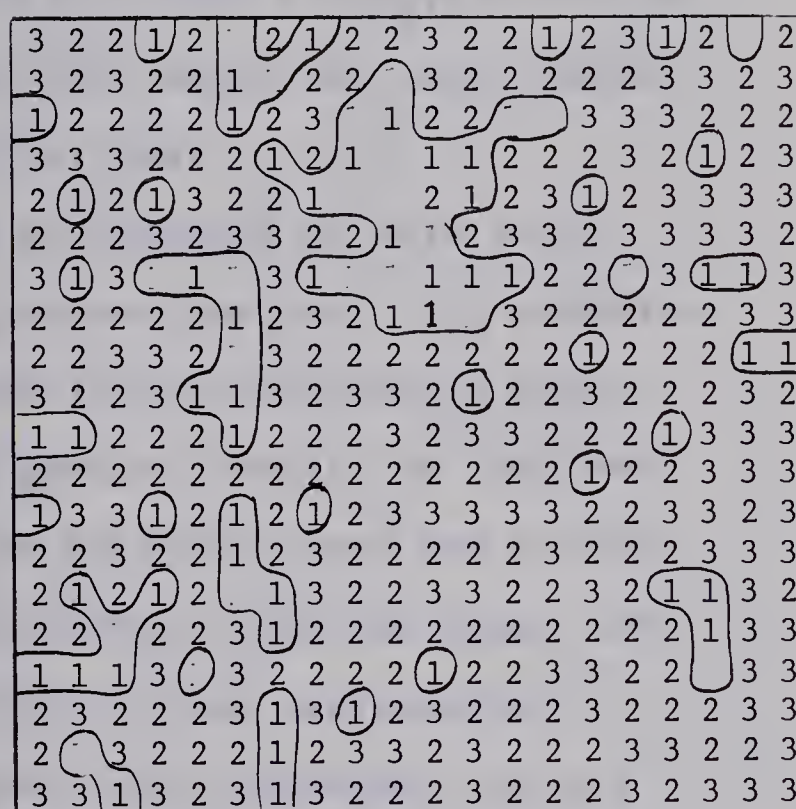


FIGURE 112

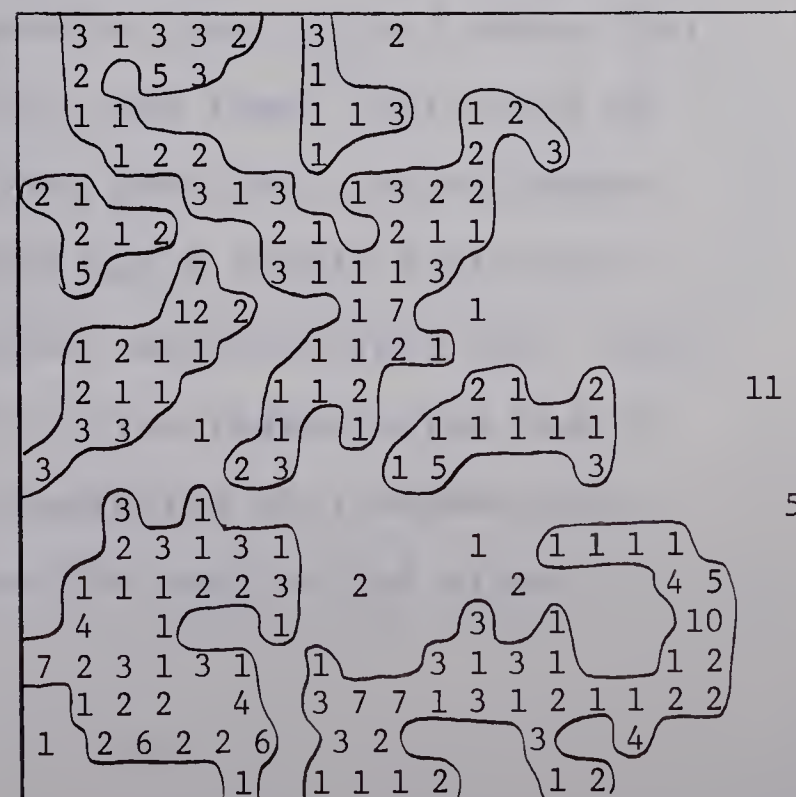
26-J-I

Pinus contorta

seedlings

numbers = actual

numbers of individuals.



In areas of older *Picea* numerous dead individuals are to be found, indicating that the *Picea* is not very long-lived here. Because of the usually greater longevity of the pine in the absence of fires in the Parks, the present pine forest may persist as an overstory to the *Picea mariana* for a very long time.

If fire should not occur here, this area will probably develop into a *Picea glauca/engelmannii* - *Abies lasiocarpa* forest, with some *P. mariana* (?). Many transgressives of *Abies* already occur throughout the area, and seed sources of *Picea engelmannii* are not far away.

The role of pine in the development of this forest appears to be strictly as a pioneer species. Its distribution as shown in Fig.111 bears little relation to topography except for a slightly greater density on the lower terrace indicating that in the past this area was slightly more favourable for pine reproduction than the upper terrace. The present distribution of pine reproduction, shown in Fig.112, indicates that pine seeds are not germinating well on the lower terrace, and Fig.113 shows that they have not done so for quite some time. This area of negligible germination coincides with the area of denser *Picea* as well as the area which has a nearly continuous carpet of *Pleurozium*, *Hylocomium*, and *Peltigera* spp.. Such conditions are not conducive to pine regeneration and it would be expected that this vegetation will expand with the invasion of the *Picea* into the rest of the stand.

In view of the fact that the Commission has not yet been able to establish the exact date of the Commission's decision, it is not possible to determine the date of the Commission's decision. The Commission's decision is therefore not binding on the Commission.

It is to be noted that the Commission has not yet been able to establish the exact date of the Commission's decision. The Commission's decision is therefore not binding on the Commission.

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The Commission has not yet been able to establish the exact date of the Commission's decision. The Commission's decision is therefore not binding on the Commission.

FIGURE 113

26-J-I

Pinus contorta
transgressives

numbers= actual
numbers of individuals.

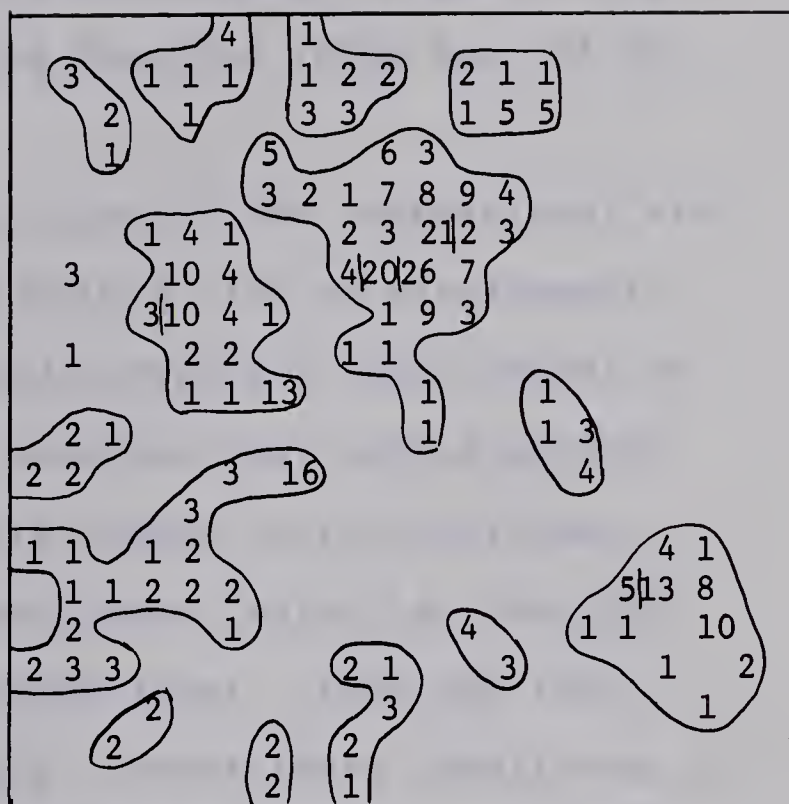


FIGURE 114

26-J-I

soil temperatures

l=low

h=high





Figure 1

Figure 1

Figure 1

Figure 1



Figure 1

Figure 1

Figure 1

Figure 1

Figure 1

Although there are numerous pine transgressives on the upper terrace, there are practically no saplings or small tree-sized individuals, indicating that the young may not be surviving.

Before leaving the discussion of the successional status of this stand, another possible line of development must be mentioned. This stand contains a large amount of standing dead pine. It was observed that during periods of strong wind, (and these are common in the Whirlpool Valley) large numbers of these trees, which had decaying bases, were broken off at ground level. Thus the tree canopy is being opened rapidly. Under these conditions, and in areas where the *Picea* does not form a dense understory, the pine may become re-established. This state of canopy opening may be a relatively recent condition occurring only when the mature pines become senescent and die. As stated earlier, although there are extremely few sapling pines, there are also extremely few dead transgressives--certainly far fewer than would be expected if reproduction were actually dying at this stage. Thus by means of a "gap-phase" type of replacement (Watt 1947), the pine may actually be regenerating as the old forest breaks up (see p.105).

THE SUBORDINATE STRATA

The distributions of many subordinate species show good positive and negative correlations with the distribution

patterns of *Picea mariana* (all size classes) and to a lesser extent with *Pinus*. The presence of *Picea* causes the micro-habitat to be cooler and perhaps moister than in more open areas lacking *Picea*. When the distribution patterns of soil temperatures measured on one day (Fig.108) are compared with the distribution pattern of the *Picea* (Fig.101 and 104), it is clear that temperatures are lower in areas of dense *Picea*. Thus species which are restricted to or reach their greatest abundance in these cooler areas may do so either because of the particular temperature, light, moisture or combination of these factors produced by the presence of the *Picea*. All of the following species are most abundant in the areas of greatest *Picea* cover

Arnica cordifolia 115

Cornus canadensis 142

Geocaulon lividum 116

Ledum groenlandicum 119

Hylocomium splendens 121

Pleurozium schreberi 123

Ptilium crista-castrensis 126

In contrast, the following:

Arctostaphylos uva-ursi 118 *Spiraea lucida* 129

Aster conspicuus 127

Calypso bulbosa 124

Solidago multiradiata 125 *Shepherdia canadensis* 127

Vaccinium caespitosum 128

are most abundant and show their greatest vigour in the warmer, presumably drier and less shady sites.

Figs. 121, 123 indicates that *Hylocomium* and *Pleurozium*

FIGURE 115

Arnica cordifolia

26-J-I

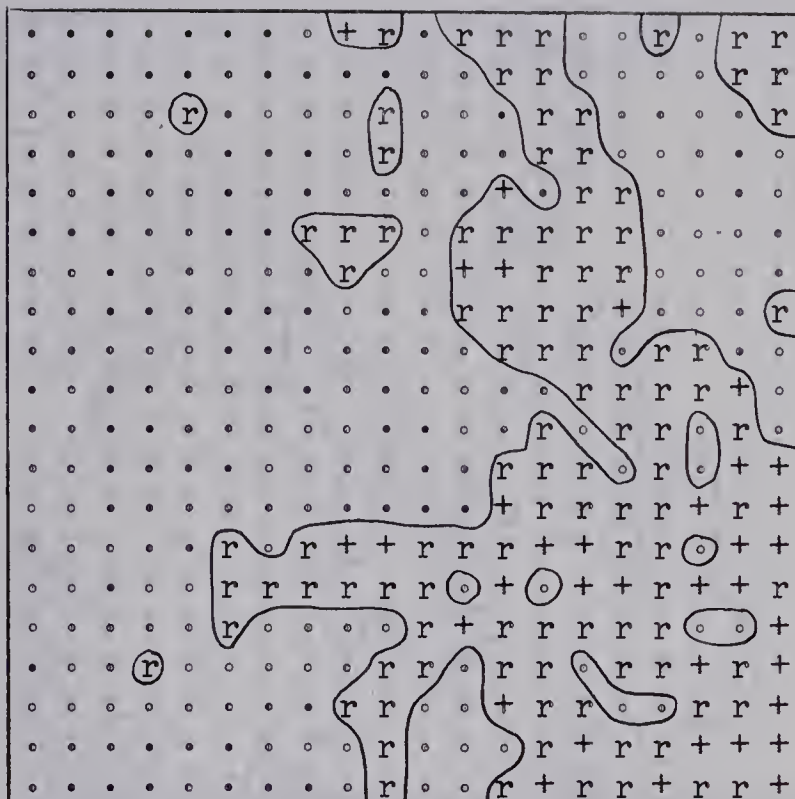


FIGURE 116

Geocaulon lividum

26-J-I

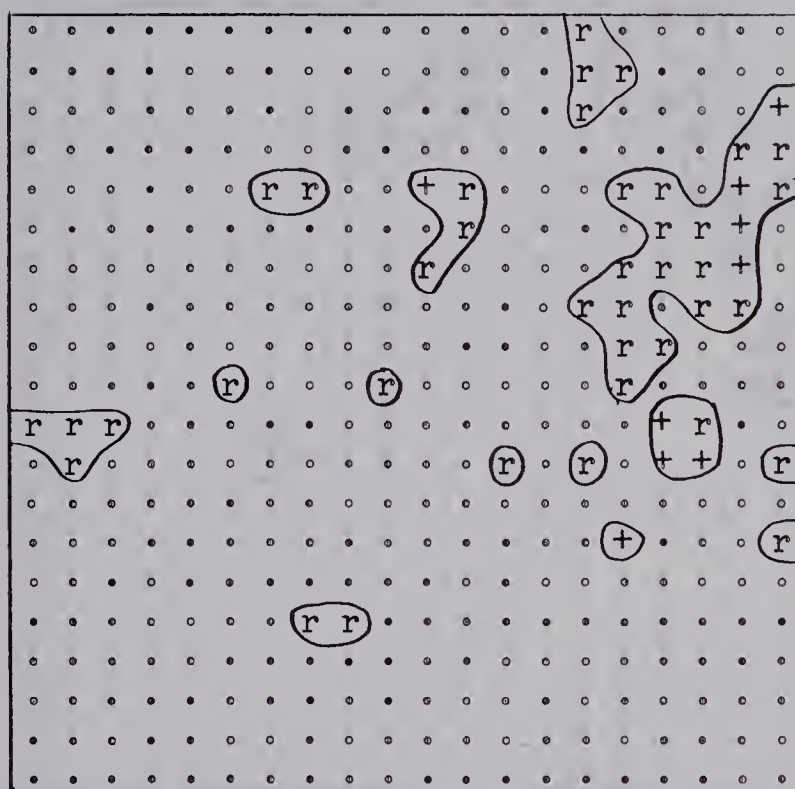


FIGURE 117

Lathyrus ochroleucus

26-J-I

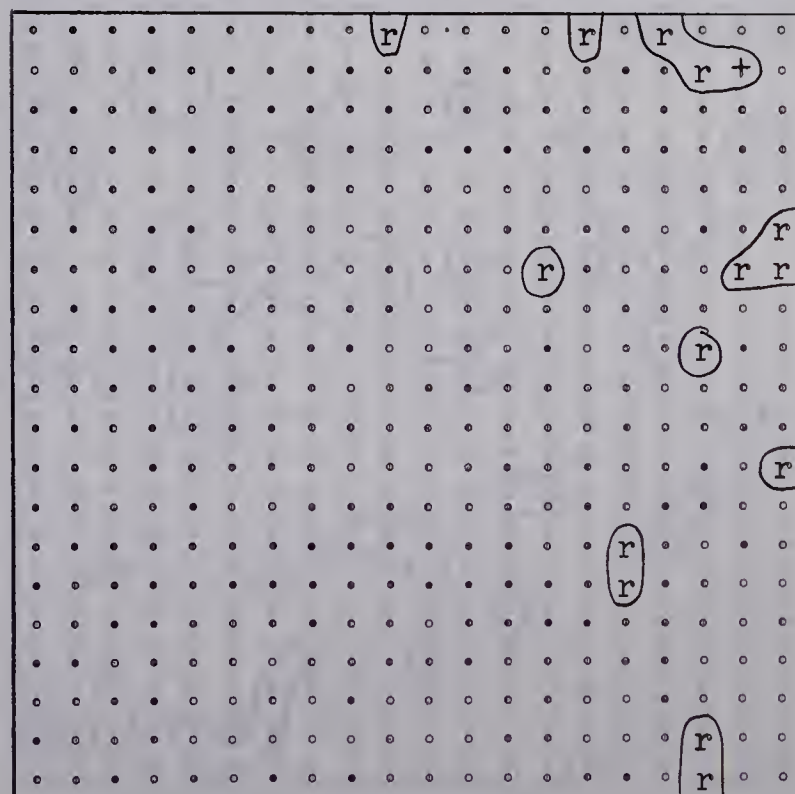




FIGURE 118

Arctostaphylos uva-ursi

26-J-I

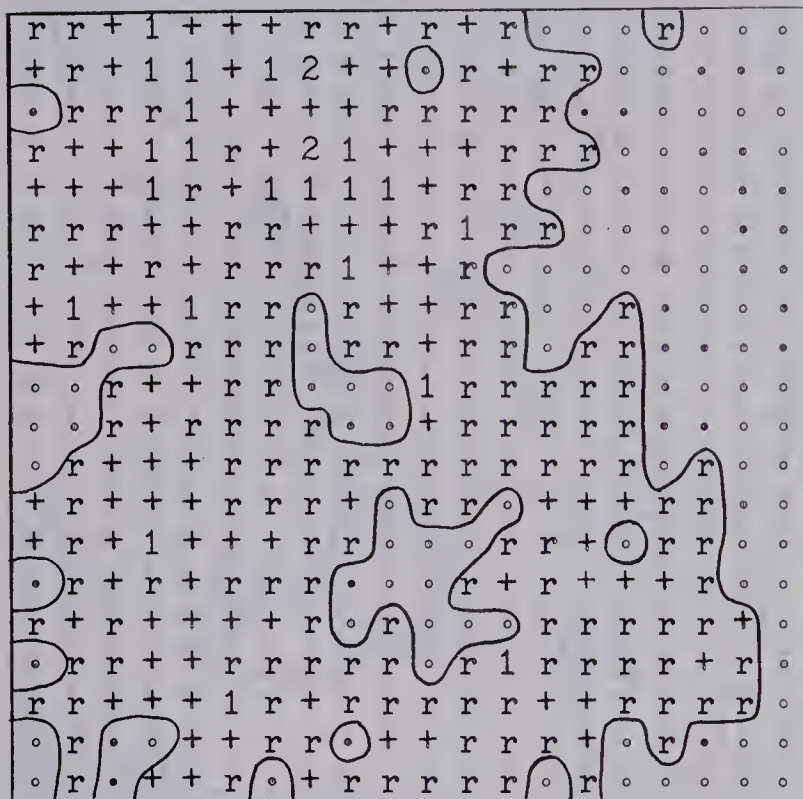


FIGURE 119

Ledum groenlandicum

26-J-I

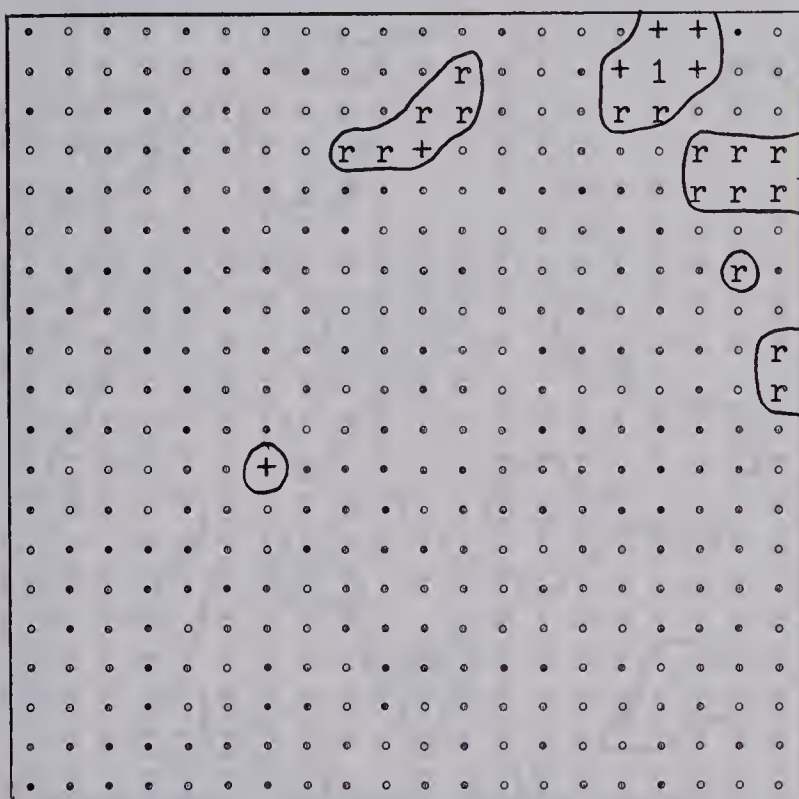


FIGURE 120

Peltigera spp.

26-J-I

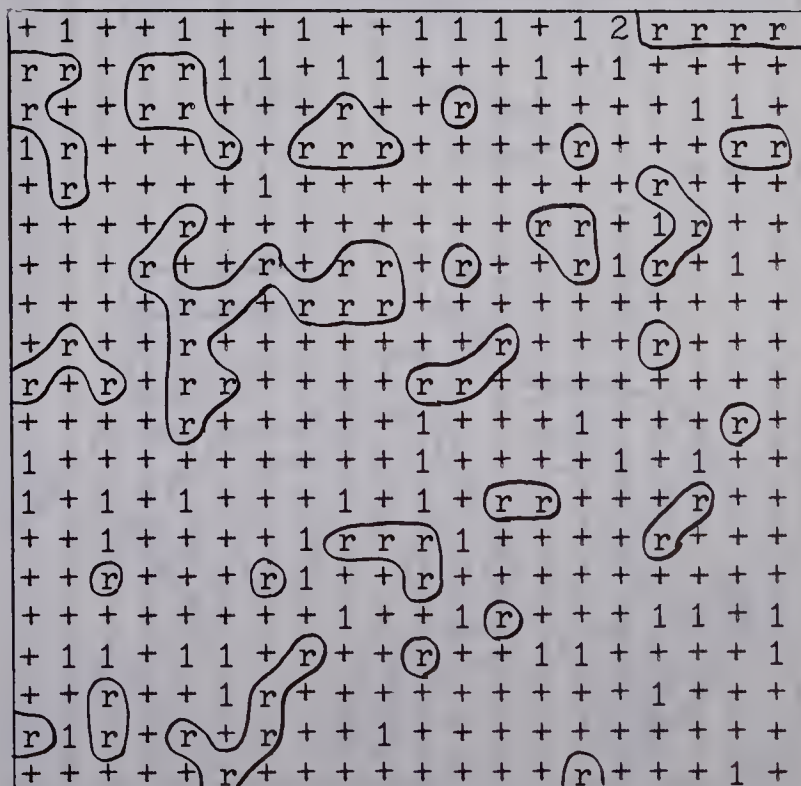


FIGURE 121

Hylocomium splendens

26-J-I

| | | | | | | | | | | | | | | | | | | | | |
|-----|-----|---|-----|---|-----|-----|-----|-----|---|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|
| 3 | (5) | 3 | 1 | + | 2 | 1 | 1 | 1 | + | 1 | + | 4 | 6 | 5 | 4 | 6 | 6 | 6 | 6 | |
| 3 | (4) | 3 | 2 | 1 | r | 1 | r | r | + | r | r | 1 | (2) | 4 | 4 | 5 | 6 | 6 | 6 | |
| 2 | 1 | 1 | + | 2 | 1 | 2 | + | 1 | 1 | 2 | 3 | 1 | (4) | 6 | 6 | 6 | 6 | 6 | 6 | |
| + | r | 1 | + | r | + | + | + | + | + | 1 | + | r | 1 | 2 | (4) | 6 | 5 | 5 | 6 | 5 |
| 3 | 1 | + | r | r | + | 1 | 1 | 2 | 1 | + | 1 | 1 | 3 | (5) | 6 | 5 | 6 | 4 | 5 | |
| r | r | + | 1 | + | 2 | (4) | r | r | + | + | r | 1 | (4) | 5 | 5 | 6 | 6 | 5 | 6 | |
| r | r | 2 | 3 | 1 | + | 3 | 1 | 1 | r | r | 1 | 1 | 2 | (5) | 5 | 4 | 6 | 5 | 5 | |
| 1 | r | r | 3 | 1 | + | 1 | 2 | r | 2 | 1 | (4) | 2 | 2 | (5) | 5 | 5 | 6 | 6 | 5 | |
| r | r | + | + | 1 | 1 | + | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 3 | (5) | 6 | 5 | 6 | 6 | |
| r | 1 | + | + | 1 | 1 | 2 | 3 | (4) | 3 | 1 | 1 | 3 | 2 | 2 | 3 | (4) | 5 | 5 | 6 | |
| + | 1 | + | + | 3 | 2 | 1 | 3 | (4) | 4 | 1 | + | 1 | (4) | 2 | 3 | (4) | 5 | 6 | 6 | |
| 1 | + | r | r | + | + | + | (4) | 5 | 2 | 1 | 2 | 3 | 3 | 3 | (4) | 4 | 4 | 5 | 6 | |
| 1 | r | 1 | 2 | 1 | 1 | + | 2 | 2 | 3 | 2 | 3 | (4) | 2 | 3 | 1 | 2 | 2 | (5) | 5 | |
| r | r | + | + | r | r | 1 | 3 | (5) | 6 | 5 | 1 | 1 | + | (4) | 6 | 6 | 5 | 6 | 6 | |
| + | 1 | 2 | 1 | r | (4) | 2 | 2 | 4 | 5 | 4 | 2 | 1 | + | + | 3 | (4) | 5 | 6 | 6 | |
| r | 2 | 3 | 3 | + | 3 | 4 | 4 | 4 | 5 | 5 | + | 2 | 1 | 3 | 3 | 1 | 1 | 3 | (5) | |
| 1 | 2 | 1 | 2 | 1 | (4) | 5 | 6 | 5 | 3 | 2 | 2 | 1 | 1 | (5) | 5 | r | r | (4) | 5 | |
| 3 | 1 | 2 | 1 | + | + | + | 1 | 1 | 1 | 1 | + | + | 1 | + | + | 1 | (4) | 6 | | |
| (5) | 3 | 1 | + | r | 2 | r | + | + | 2 | 1 | 1 | 2 | 3 | 2 | 2 | 1 | 3 | (5) | 5 | |
| (4) | 1 | 3 | (4) | 1 | 3 | + | + | + | 3 | 1 | 3 | 1 | 3 | 2 | + | 3 | (5) | 6 | 5 | |

FIGURE 122

Dicranum polysetum

26-J-I

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| r | + | r | r | r | r | r | + | r | r | r | + | + | r | r | r | r | . | r | . |
| + | r | r | r | r | r | r | + | + | + | + | + | + | r | . | r | . | . | r | r |
| r | r | + | + | r | + | r | r | r | + | r | r | r | . | . | . | r | r | . | |
| + | r | + | r | + | + | r | r | r | + | 1 | + | + | + | r | . | . | r | . | . |
| r | r | r | 1 | + | + | r | r | r | + | + | + | + | + | r | r | r | . | . | . |
| + | + | + | + | r | + | + | + | + | + | + | + | + | + | r | . | r | r | r | r |
| 1 | 1 | r | + | r | + | r | + | + | 1 | + | r | + | r | r | r | r | r | r | + |
| r | r | + | r | + | r | r | r | + | r | r | + | + | + | r | r | + | r | r | r |
| + | + | + | + | r | + | r | + | + | 1 | r | + | + | + | r | r | r | . | r | r |
| + | + | r | r | r | r | r | r | + | r | r | r | + | + | + | 1 | r | . | . | r |
| r | + | r | r | + | + | + | r | + | + | + | + | + | + | + | + | + | + | + | r |
| + | r | r | + | + | + | + | r | + | + | 1 | + | + | + | r | + | + | + | + | r |
| + | + | r | r | r | r | + | + | + | r | + | + | + | r | r | r | + | 1 | + | r |
| r | r | r | r | r | + | + | r | r | r | r | 1 | + | + | + | r | r | + | r | r |
| + | + | r | r | + | r | r | + | + | r | r | r | r | 2 | . | r | r | r | r | r |
| + | r | r | r | + | r | r | r | . | . | r | r | r | r | r | r | r | r | r | r |
| r | r | r | r | r | r | r | r | r | + | r | + | + | + | r | r | r | r | + | r |
| + | r | r | r | + | r | r | r | r | + | r | r | r | r | r | + | + | + | + | r |
| r | r | r | + | + | r | + | + | r | + | r | r | r | r | + | + | + | r | r | r |
| r | r | r | r | + | r | + | r | r | r | + | r | r | r | r | r | r | r | r | r |

FIGURE 123

Pleurozium schreberi

26-J-I

| | | | | | | | | | | | | | | | | | | | |
|-----|---|-----|-----|-----|---|-----|---|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|---|---|
| 1 | 1 | 1 | (3) | + | 2 | 2 | 1 | 2 | 1 | (4) | 2 | 1 | + | + | 1 | + | + | + | r |
| 2 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | + | (3) | 1 | + | r | 1 |
| 2 | 2 | 2 | + | 2 | 2 | (3) | 2 | 2 | 2 | 2 | (4) | 2 | 1 | 1 | 1 | + | 1 | + | r |
| 2 | 2 | 2 | 2 | + | + | + | + | + | 1 | 1 | (3) | 4 | (3) | + | 1 | 2 | 2 | + | 1 |
| 2 | 2 | 2 | 1 | r | + | 1 | 1 | 1 | 1 | 1 | 1 | 1 | + | + | r | 1 | r | r | + |
| 1 | 1 | 1 | + | + | 2 | 2 | + | 1 | + | + | r | 1 | + | r | r | 1 | r | + | 1 |
| 1 | 2 | 2 | 2 | 1 | 2 | 1 | 2 | + | + | + | 1 | 2 | 1 | 1 | r | 1 | r | r | 1 |
| 2 | + | 1 | (3) | 3 | 3 | 3 | 3 | 2 | 1 | 2 | (3) | 2 | 2 | + | + | r | 1 | + | 1 |
| 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | r | r | r | + |
| 2 | 1 | 2 | (3) | 3 | 2 | 3 | 2 | 3 | 3 | 3 | 4 | 3 | 2 | 2 | 2 | r | r | + | r |
| 1 | 2 | 1 | 2 | 2 | 3 | 3 | 3 | 2 | 4 | (2) | 4 | 4 | 3 | 3 | 3 | 3 | 1 | + | 1 |
| 2 | 2 | 3 | 3 | 3 | 1 | 2 | 2 | 3 | 5 | (2) | 4 | 4 | (2) | 1 | 3 | 4 | (3) | 1 | + |
| 2 | 4 | 4 | 4 | (2) | 1 | 4 | 4 | 4 | 3 | 4 | 3 | 3 | 5 | 3 | 3 | 3 | 2 | 1 | 1 |
| 4 | 5 | 5 | (1) | 3 | 1 | 2 | 3 | 2 | 1 | 2 | 5 | 5 | 4 | 3 | + | + | 1 | + | + |
| 5 | 5 | 3 | 3 | 2 | 1 | 3 | 3 | 2 | 2 | (3) | 3 | (2) | 3 | 3 | 3 | 1 | 1 | r | r |
| 2 | 3 | 3 | 3 | 3 | 2 | 1 | 1 | 2 | 1 | 2 | 3 | 3 | 3 | 3 | 3 | 2 | (4) | 1 | |
| 3 | 3 | 3 | 3 | 3 | 2 | + | r | 1 | (3) | 2 | 2 | 2 | 3 | (1) | 1 | 4 | 3 | 2 | 1 |
| 3 | 3 | (2) | + | + | 1 | 1 | 1 | 2 | 3 | 2 | 3 | 4 | 4 | 3 | (4) | 2 | 3 | 1 | r |
| (1) | 3 | 4 | 3 | 1 | 2 | r | + | (3) | 2 | 3 | 4 | 3 | 3 | 3 | (2) | 4 | 2 | 1 | + |
| 3 | 4 | 3 | 3 | 3 | 2 | 2 | 1 | 2 | 3 | 5 | 4 | 4 | 3 | 3 | 4 | 2 | 1 | r | r |



100-100000
100-100000
100-100000

100-100000
100-100000
100-100000

100-100000
100-100000
100-100000

FIGURE 124

Calypso bulbosa

26-J-I

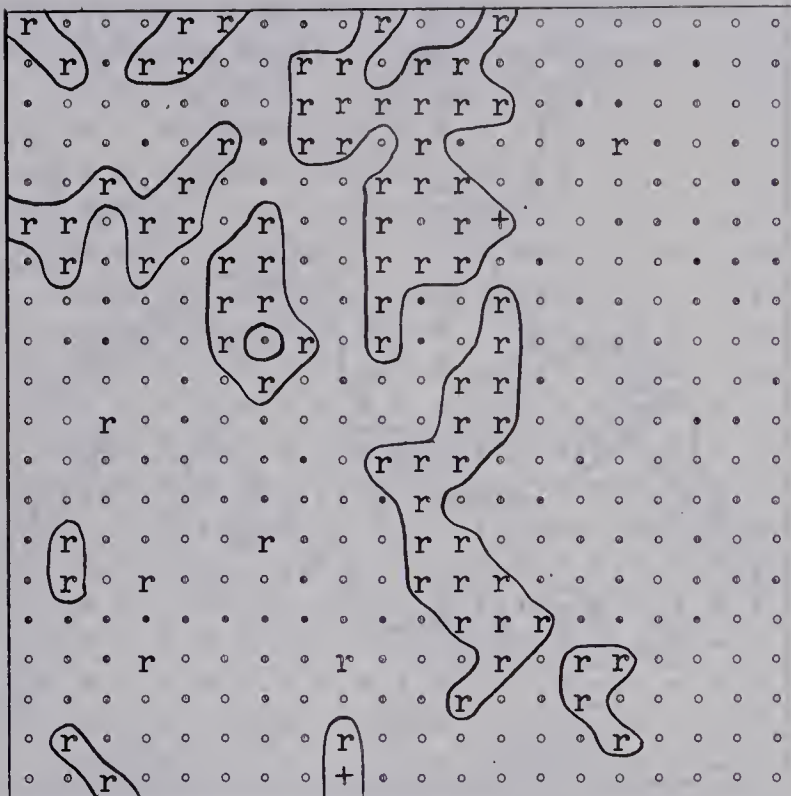


FIGURE 125

Solidago multiradiata

26-J-I

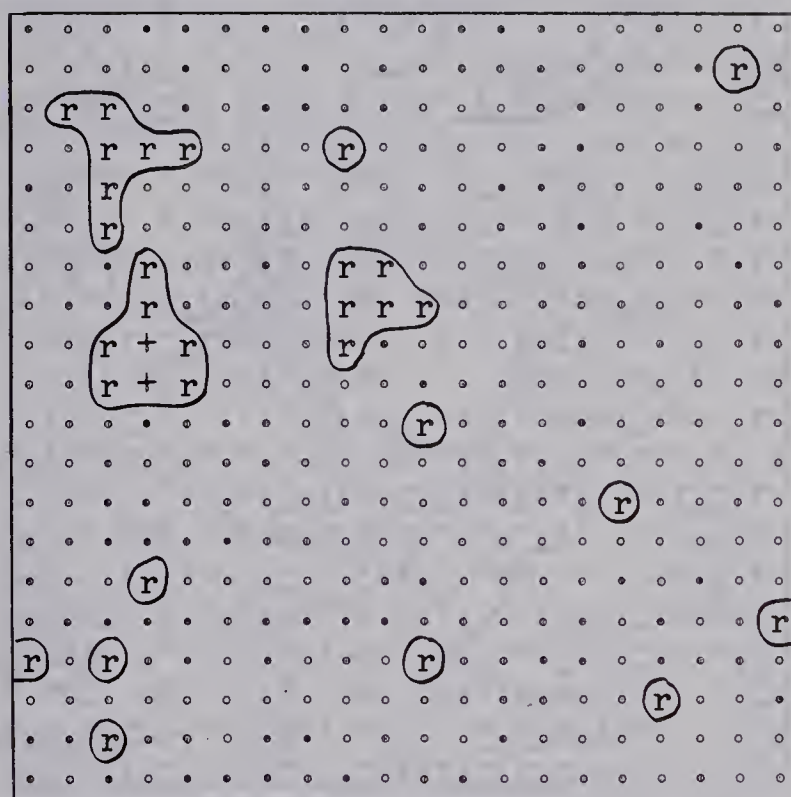


FIGURE 126

Ptilium crista-castrensis

26-J-I

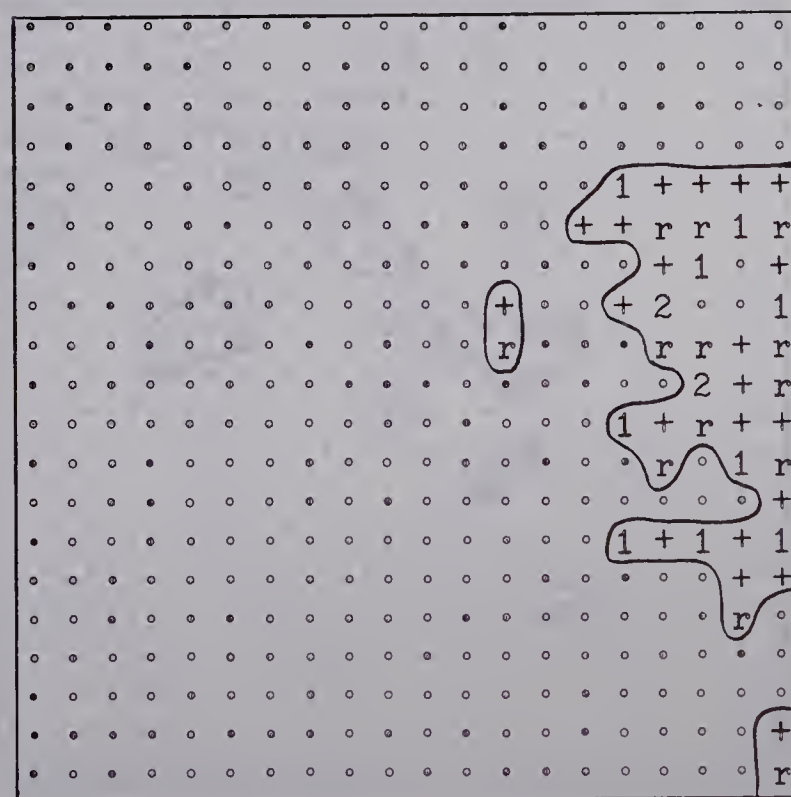


FIGURE 127

Shepherdia canadensis

26-J-I

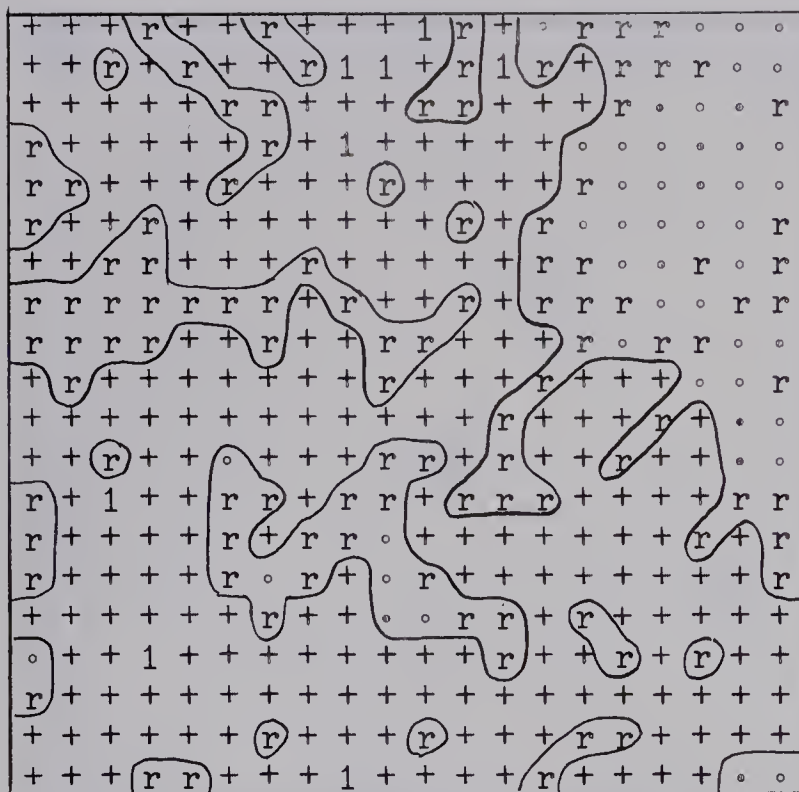


FIGURE 128

Vaccinium caespitosum

26-J-I

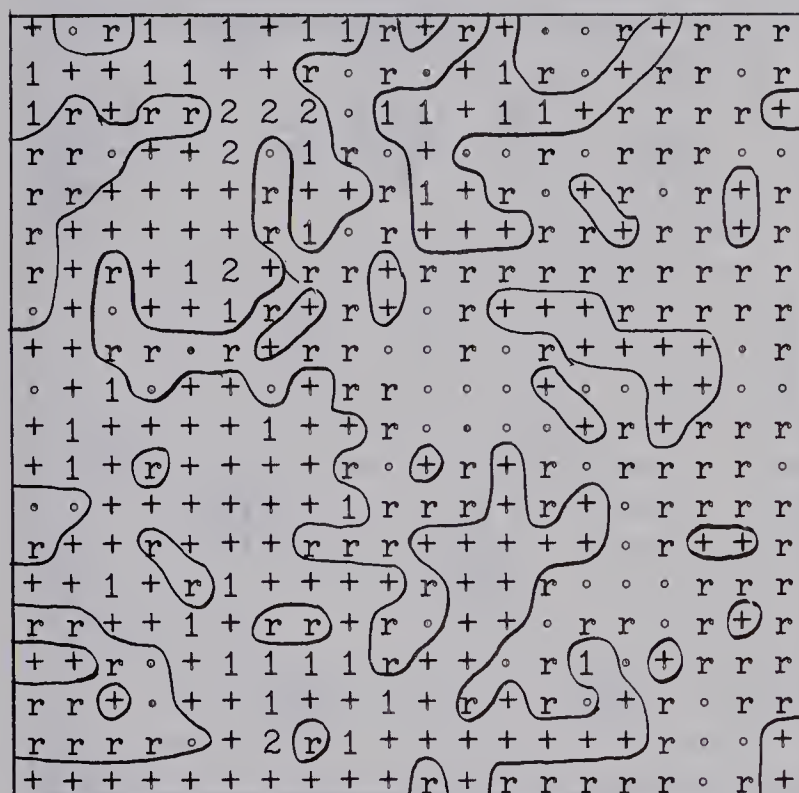


FIGURE 129

Spiraea lucida

26-J-I

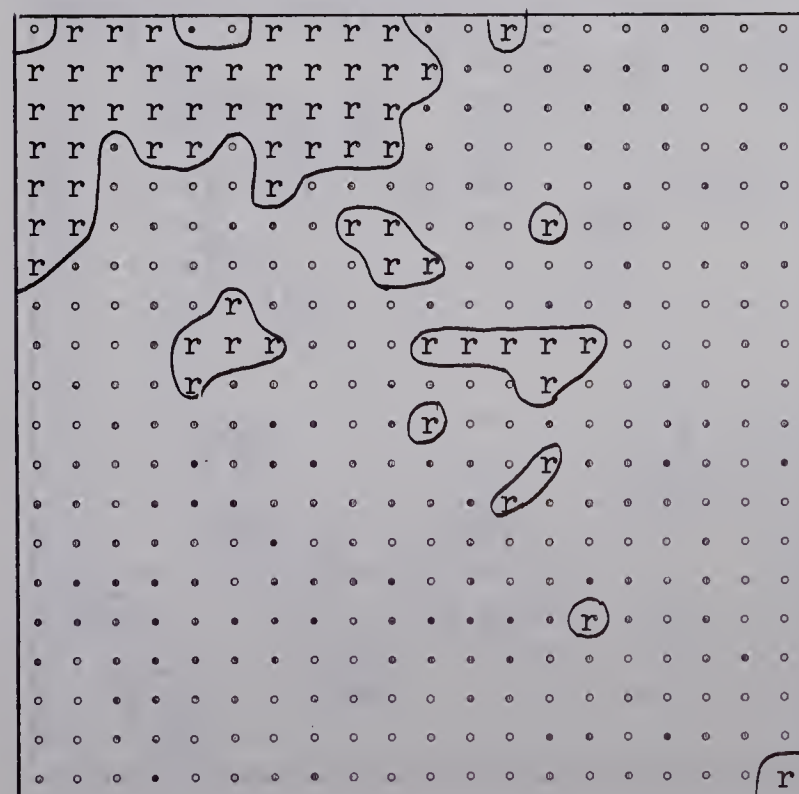


FIGURE 133

Aster conspicuus

26-J-I

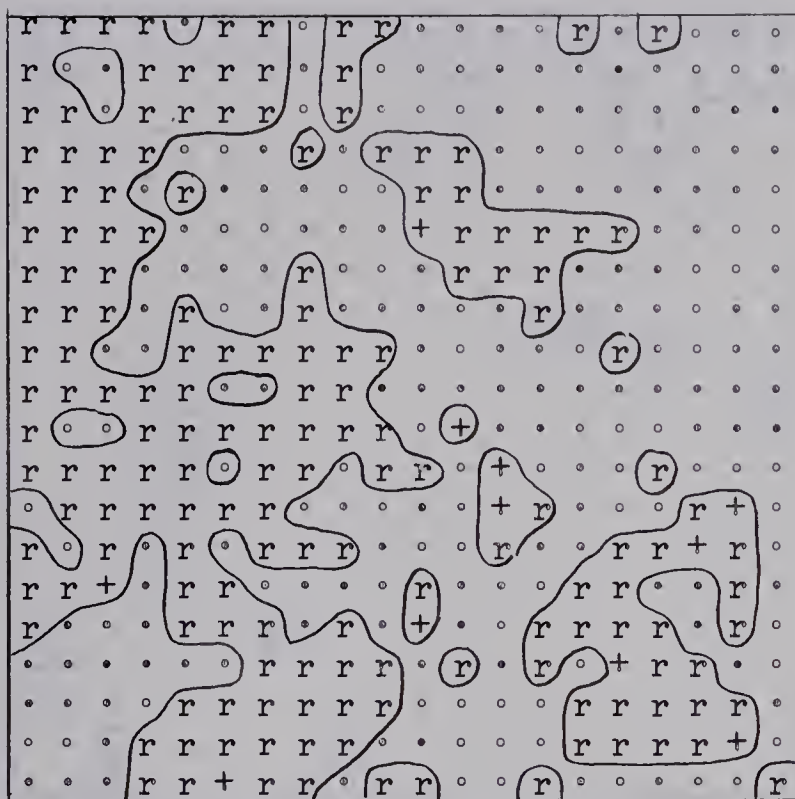


FIGURE 134

Pyrola secunda

26-J-I

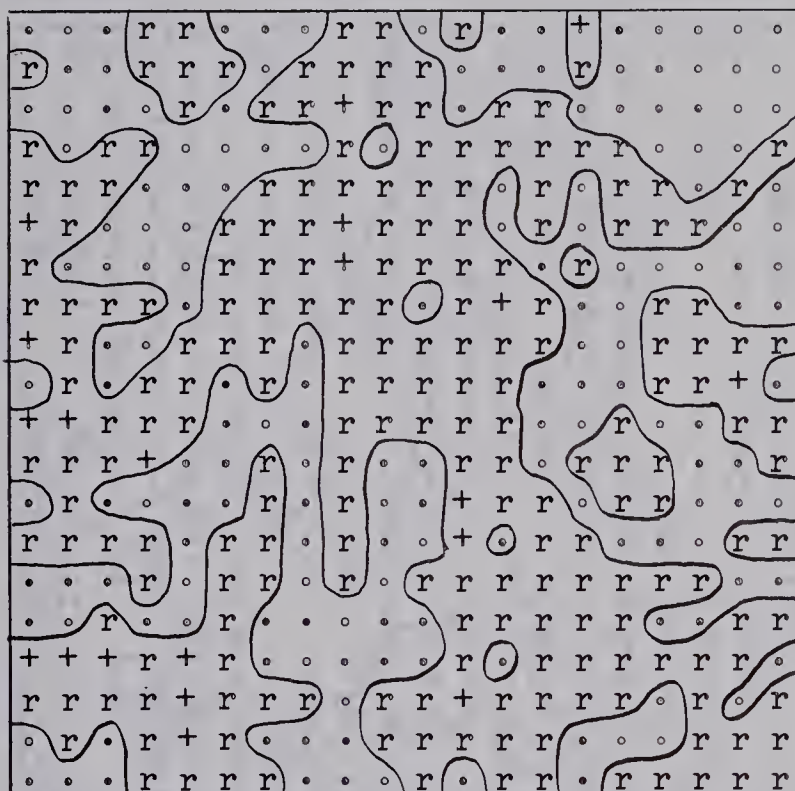


FIGURE 135

Campanula rotundifolia

26-J-I

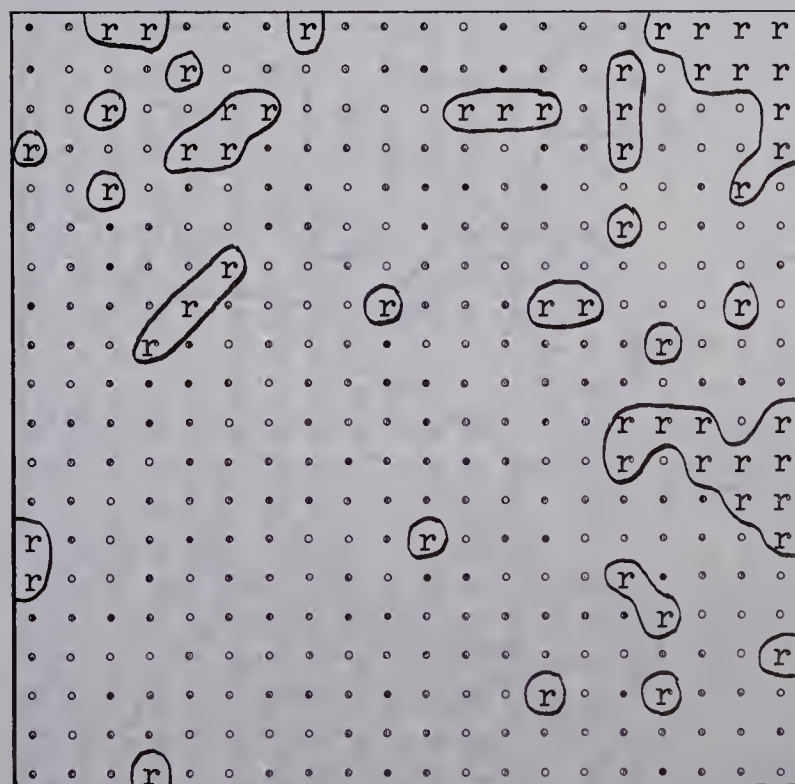


FIGURE 136

Epilobium angustifolium

26-J-I

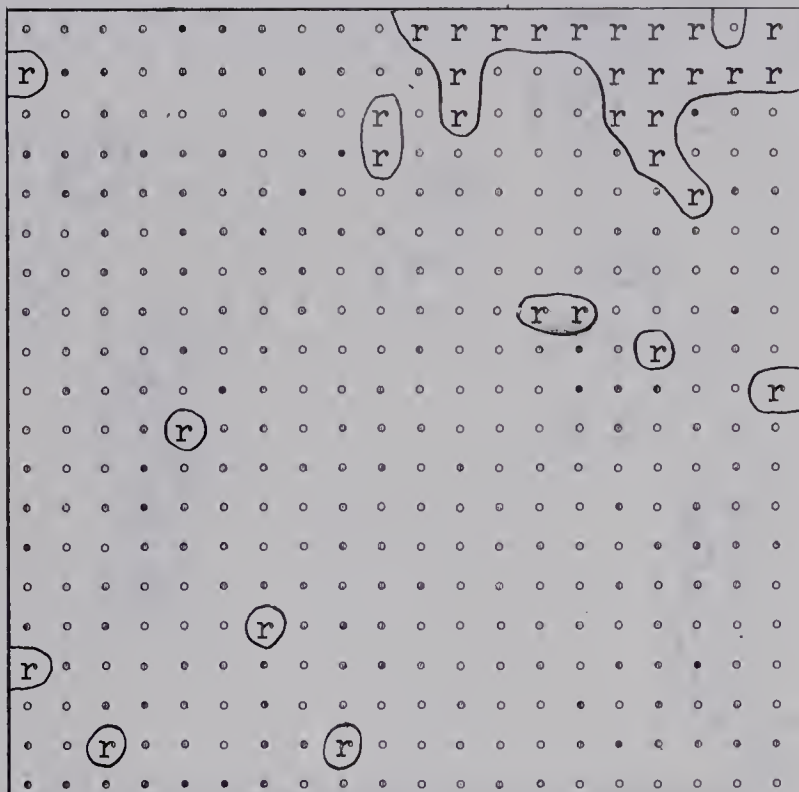


FIGURE 137

Juniperus communis

26-J-I

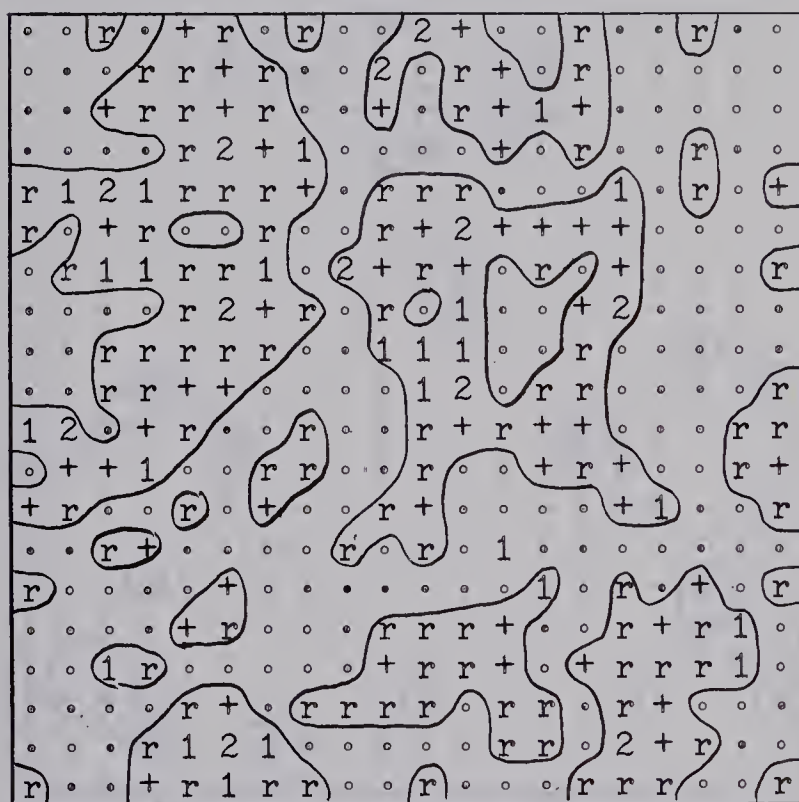


FIGURE 138

Pyrola virens

26-J-I

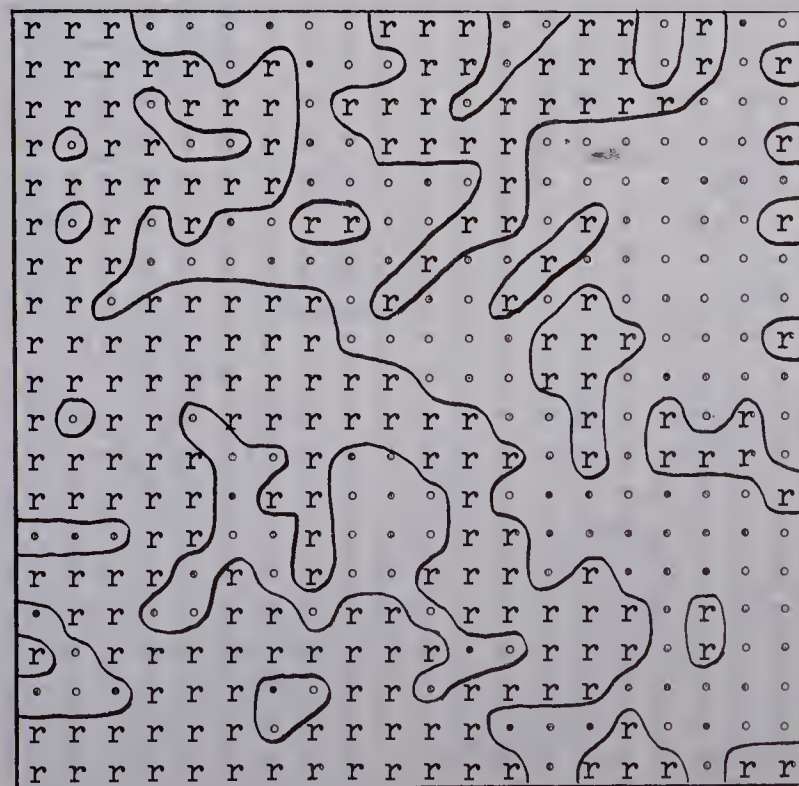


FIGURE 139

Achillea millefolium

26-J-I

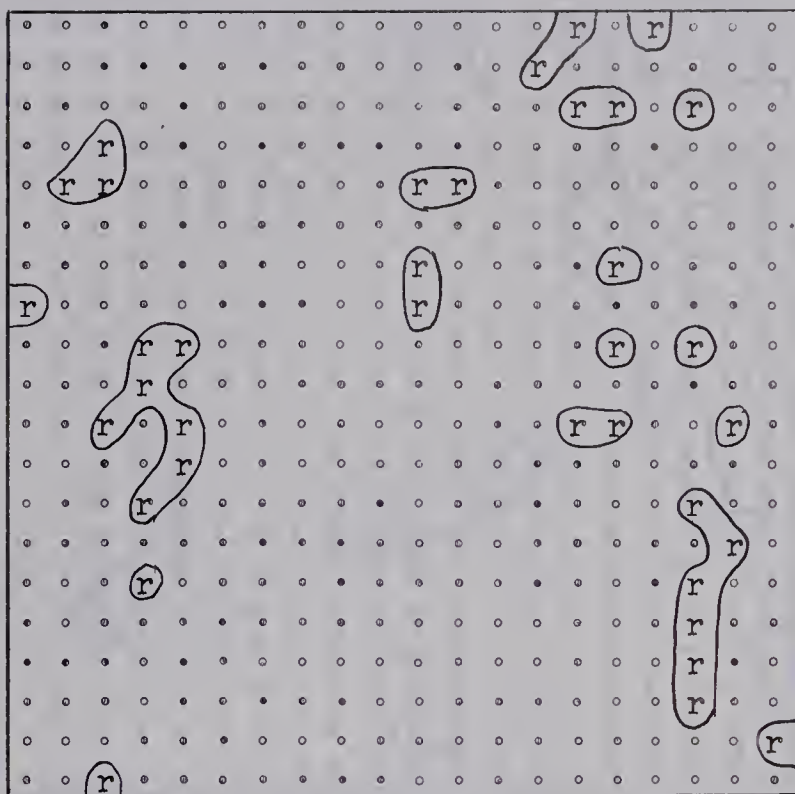


FIGURE 140

Fragaria virginiana

26-J-I

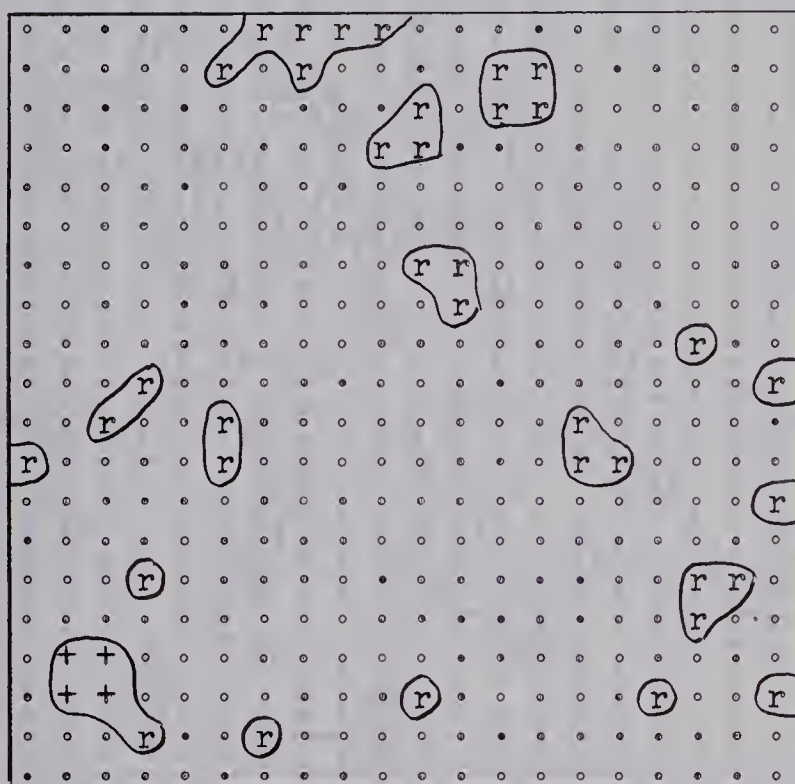


FIGURE 141

Rosa acicularis

26-J-I

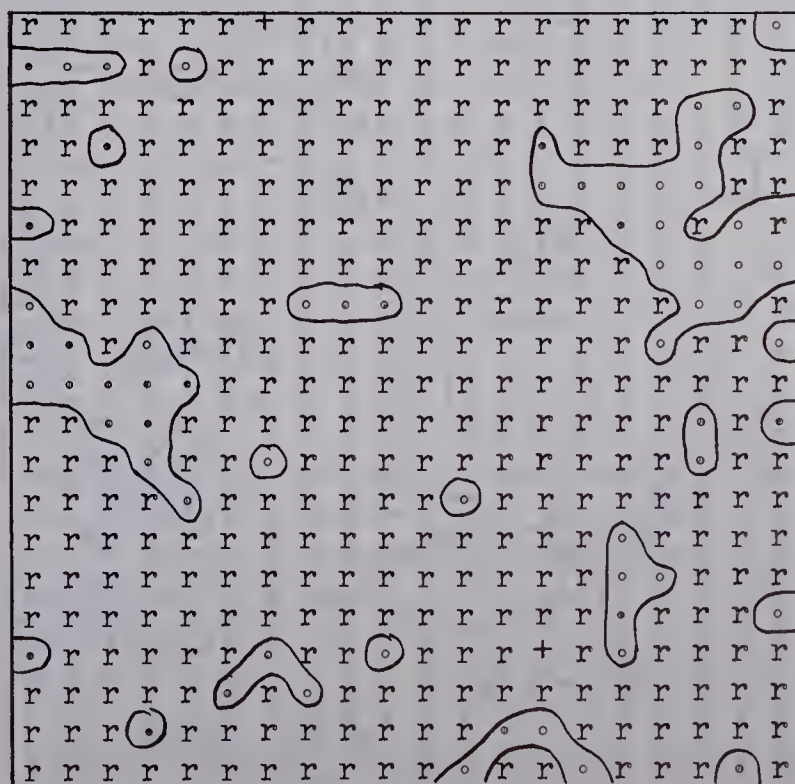


FIGURE 142

Cornus canadensis

26-J-I

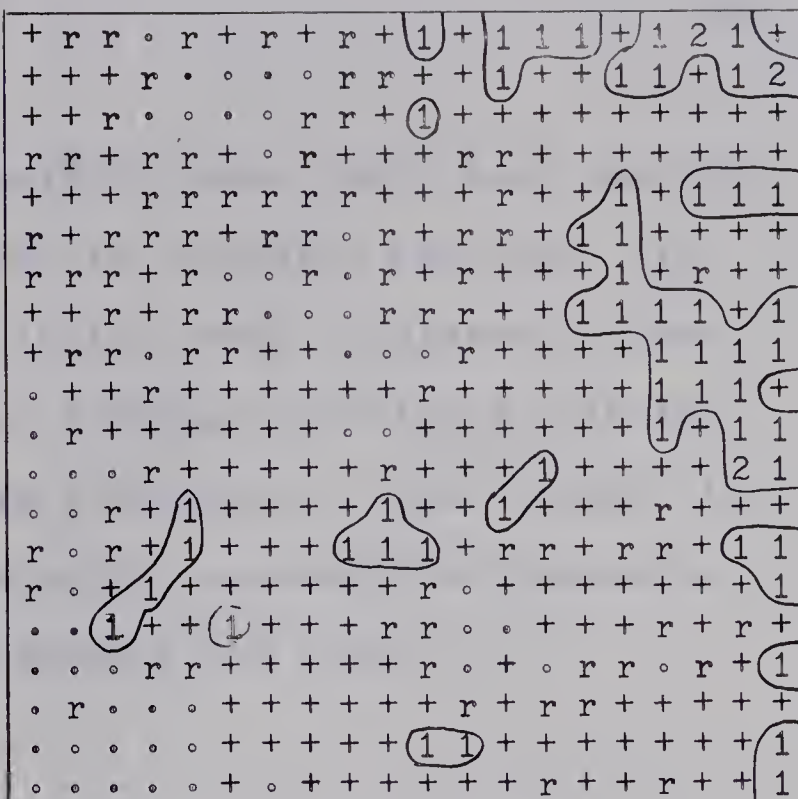


FIGURE 143

Linnaea borealis

26-J-I

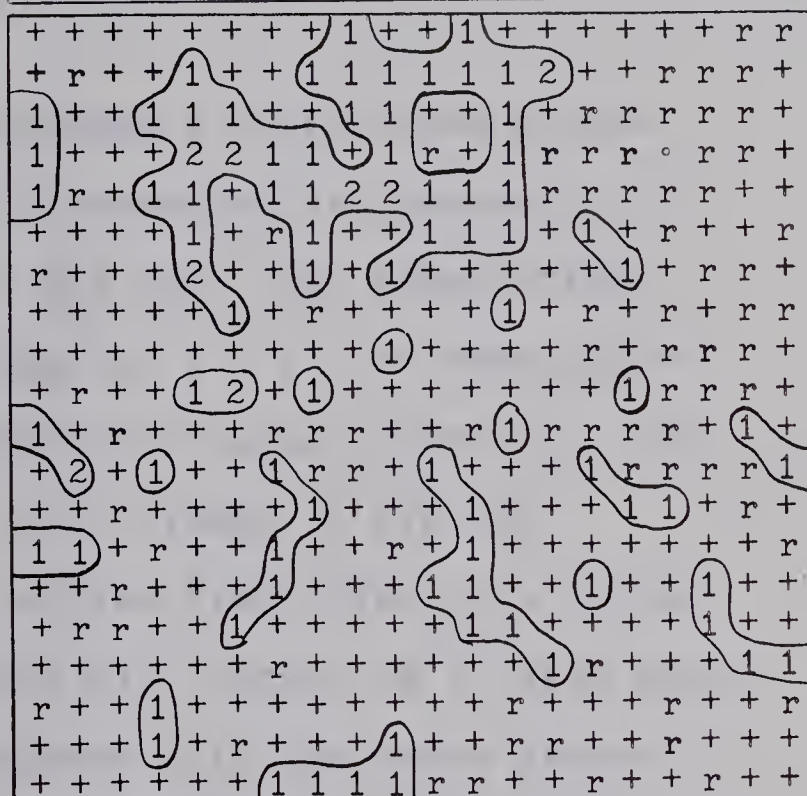
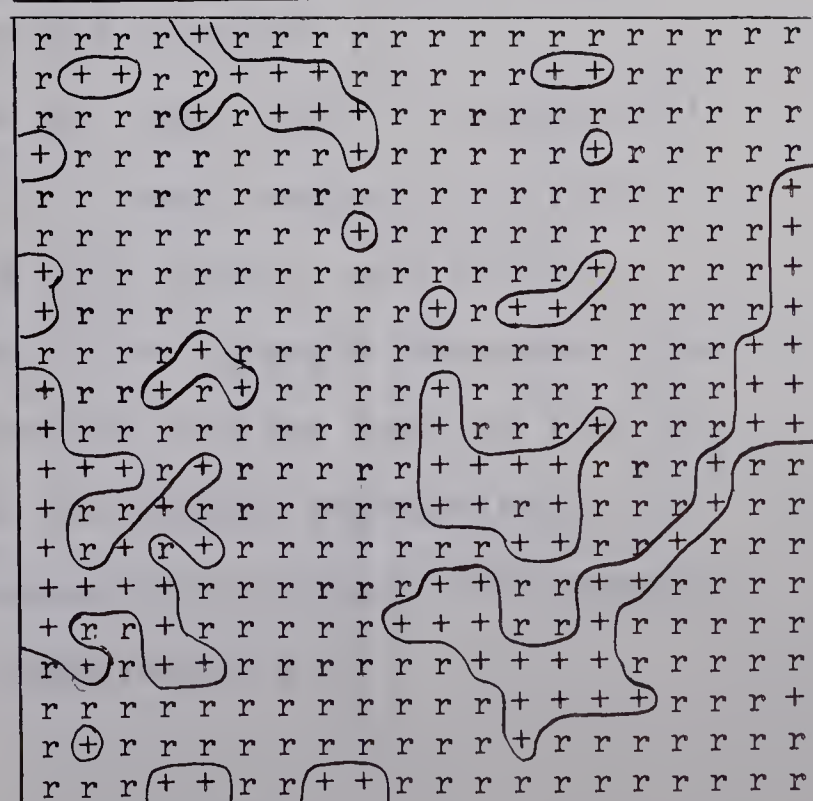


FIGURE 144

Elymus innovatus

26-J-I



although often occurring together, reach their best development (here indicated by cover) in different habitats. The *Hylocomium* is most abundant in the areas of greatest *Picea* cover whereas the *Pleurozium*, although associated with the *Picea*, is most abundant where the spruce is less dense. It is possible that the *Hylocomium* may succeed the *Pleurozium* as the *Picea* increases in abundance and cover.

4. 55-J-I: TREE STRATUM

The pine trees are contagiously distributed within the stand. Several levels of contagion are present, of which only one is evident in Fig.145. The pines either occur singly or in small groups of 2 - 5. In some places these groups are close together and larger groups 15 - 20 m across are formed. These are evident in Fig.145. On a scale larger than that of the study plot is a third level of contagion. The study plot occurs in a large area which is relatively open compared with the dense groups of pines which also occur on the terrace.

The successional status of stand 55-J-I is difficult to interpret at the present. In many respects (listed below) it resembles a climax pine forest, and yet the maintenance of this apparent climax appears dependent upon the chance juxtaposing of certain factors such as the availability of viable seed, low rodent populations so that seed harvesting is lessened, favourable environmental conditions of moisture and temperature *etc.*.

179

trees

[illegible]

•

| | | | | | | |
|---|---|---|---|---|---|---|
| 1 | 1 | 6 | 2 | 2 | 1 | 1 |
| | | | | 1 | | |
| | | 1 | | | 1 | |
| | | | | | | |
| 1 | | | | 1 | | 1 |
| | | | | | 1 | |
| 1 | | | | | | 1 |
| | 1 | | | 1 | | 1 |
| | 1 | | | 3 | 1 | 1 |
| | | | | | | 1 |
| | | | | | | |
| | | | | | | 1 |

1

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|

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| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|

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| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|

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| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|

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|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|

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| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|

The climax features of the tree stratum of this stand have been discussed in different contexts in previous sections, but are summarized below:

1. the density-diameter distributions (Fig. 10 and 17) show a mature tree stratum with ample reproduction of the same species to replace loss due to mortality in the trees;
2. there is a wide range of ages in the pine trees (Fig. 10) which is typical of climax, not seral forests;
3. reproduction of other tree species is very low (Table 14) and the few individuals present are confined to the smallest size-classes which is unusual in a stand which is 75 years old;
4. the cover of pine is the lowest of the five intensive stands (18%, Table 10) therefore making pine reproduction possible beneath the tree canopy;
5. tree density is low (759/hectare) and this also increases the potential for pine reproduction.

There is some reason to doubt the climax status of stand 55-J-I. Oosting (1956, p. 252) describes a climax community as one which "...may continue indefinitely, because individuals that are lost for any reason are replaced by their own progeny.". Any loss of *Pinus* trees in 55-J-I will at present be replaced by *Pinus*, but whether this community will last indefinitely is not known with any certainty.

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| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | | |
| 1 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 3 | 2 | 2 | 3 | 2 |
| 1 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 2 | 2 | 3 | | |
| 1 | 1 | 2 | 3 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | |
| 2 | 2 | 3 | 3 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 3 | 2 | | |
| 3 | 2 | 3 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 3 | |
| 2 | 1 | 2 | 2 | 3 | 3 | 1 | 2 | 3 | 2 | 2 | 1 | 1 | 3 | 2 | 1 | 2 | 3 | | |
| 2 | 2 | 1 | 2 | 2 | 3 | 3 | 3 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | |
| 2 | 3 | 2 | 3 | 1 | 1 | 2 | 2 | 3 | 2 | 2 | 3 | 2 | 1 | 1 | 1 | 2 | 2 | 3 | 2 |
| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 2 | 1 | 2 | | |
| 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | | |
| 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 3 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | | | | |
| 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | | | | |
| 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | | | | |
| 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | | | | |
| 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | | | | |
| 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | | | | |
| 3 | 3 | 3 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | | | | |

transgressives plus
saplings

1 1 2 2 1 2 2 3 2 2 1 1 2 1
1 1 2 2 2 2 1 1 3 2 2 2 1 1 1 1
1 2 3 3 2 2 2 2 2 2 1 1 1 1
1 2 2 2 2 1 1 2 1 1 1 1 1 1
1 1 2 2 1 1 1 2 2 2 2 1 1 1 1 2 2
2 1 1 2 1 1 2 1 1 2 2 2 2 2
2 2 1 1 2 2 2 1 1 2 1 2
3 3 3 3 1 1 1 2 1 1 2 1

[illegible]

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|----|---|---|---|---|---|
| 1 | 3 | 4 | 4 | 4 | 4 | 8 | 4 | 11 | 3 | | 4 | 8 | 3 |
| | | | 2 | 4 | | | 6 | 1 | 1 | | | | |
| 2 | | | | | | | | | 1 | | | | |
| | 4 | 7 | | | | | | 7 | | | 7 | | |
| 2 | 8 | 4 | 2 | | 2 | | | | | | | | |
| | 3 | | | | | 3 | | | | | | | |
| | | | | | | | | | | | 1 | 1 | 1 |
| 2 | | | | | | | | | | | | | |
| | | 2 | | | 3 | 3 | 2 | 2 | | | | | |
| | | | | | | | | | | | | | 2 |
| | | | | | | | 3 | | | | | | |
| | | | 3 | | | | | 2 | | | | | |
| | | | | | | | | 4 | 3 | 1 | | 1 | |
| | | | | | | | | | 3 | | | | |
| | | | | | | | | 1 | | | | | |
| | | | | | | 1 | | | 1 | | | | |
| | | | | | | | 2 | | | | | | |

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2 4 7 7 1
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3
3 2 1 1
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1 2 1
1 3 3 1
1 4 6 4 1
1 5 10 10 5 1
1 6 15 20 15 6 1
1 7 21 35 35 21 7 1
1 8 28 56 70 56 28 8 1
1 9 36 84 126 126 84 36 9 1
1 10 45 120 210 252 210 120 45 10 1

2 3 3 2 2 2

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3 2 1 1

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From the distributions of both living and dead pine by size classes, the following points are notable:

1. areal distribution of the smaller size pine (age *ca.* 25 years and less) is contagious (Fig.148), *i.e.* reproduction has not been evenly distributed throughout the area;
2. there is a very large number of living pine in the small size classes (*ca.* 3,300 seedlings and 2,600 transgressives and saplings per hectare) but proportionately very few (157) dead individuals (Fig.149);
3. reproduction of other tree species is negligible.

What can be inferred from the above three points is that the abundant reproduction of pine is relatively recent *i.e.* has occurred over the last 25 - 30 years. The potential for pine regeneration is not equally high throughout the stand. The few dead saplings and transgressives occur in the areas of densest reproduction and therefore are normal mortality due to intraspecific competition.

Reasons why tree reproduction was negligible during the first 50 years of this stand are not clear at present. A climatic change from "drier" to "wetter" could be a causal factor but climatic data for the area are not available. If the conditions favouring tree reproduction continue, then a more fully stocked, uneven-age, pine forest will develop. Such a forest could, in an undetermined length of time during which both fire and

unfavourable climatic conditions were barred, develop into a *Picea-Abies* climax forest. If on the other hand, conditions which seem to inhibit tree reproduction are recurrent, then a climax-like forest dominated by *Pinus* could be maintained. Detailed work to determine past climatic conditions of this stand in addition to the construction of "life tables" (after Deevey 1947) for the tree species would greatly aid in the understanding of the successional status of this stand.

THE SUBORDINATE STRATA

The distribution of the subordinate vegetation appears to be in response to slight variation in microhabitats. On the basis of species composition and abundance, moist, mesic, and xeric areas may be recognized within the stand. The naming of such areas is not meant to indicate that they are precisely definable--they are not. Rather, a gradient of moisture conditions exists across the plot.

The northeast corner and the east side are the moistest. The occurrence of *Anemone parviflora*, *Arctostaphylos rubra*, and *Parnassia palustris* (Fig.151) indicate the presence of locally wet conditions. *Epilobium angustifolium* (Fig.153) is restricted to this moist area and *Pleurozium schreberi* (Fig.155) reaches its greatest abundance there. Other species such as:

FIGURE 151

55-J-I

Ap = *Anemone parviflora*
Ar = *Arctostaphylos rubra*
Pp = *Parnassia palustris*

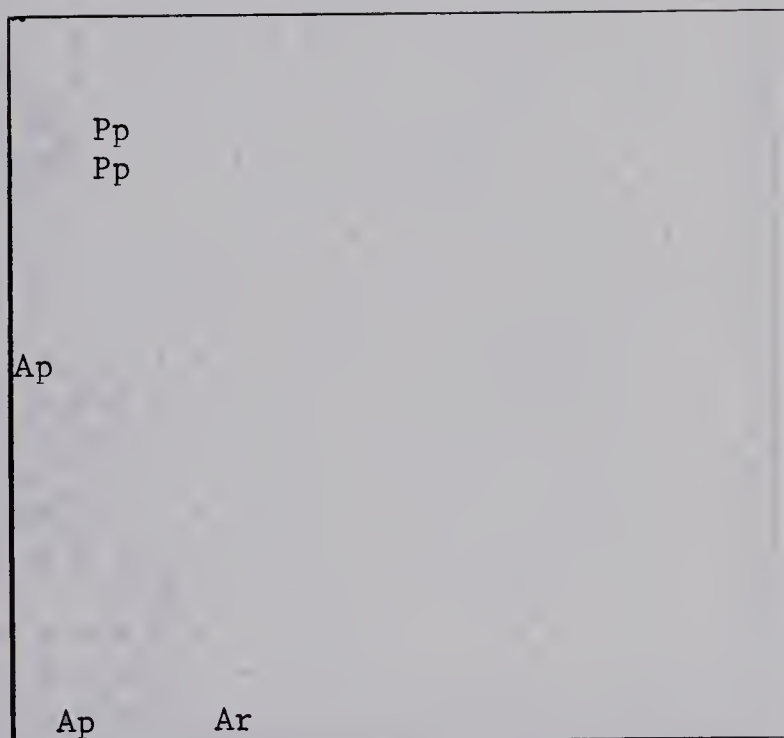


FIGURE 152

Arnica cordifolia

55-J-I

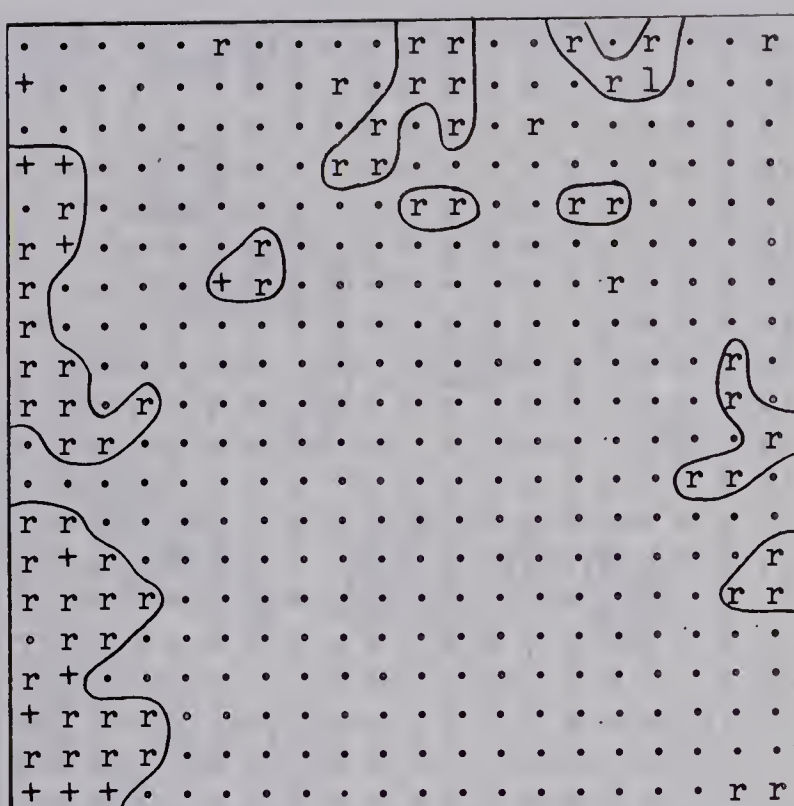


FIGURE 153

Epilobium angustifolium

55-J-I

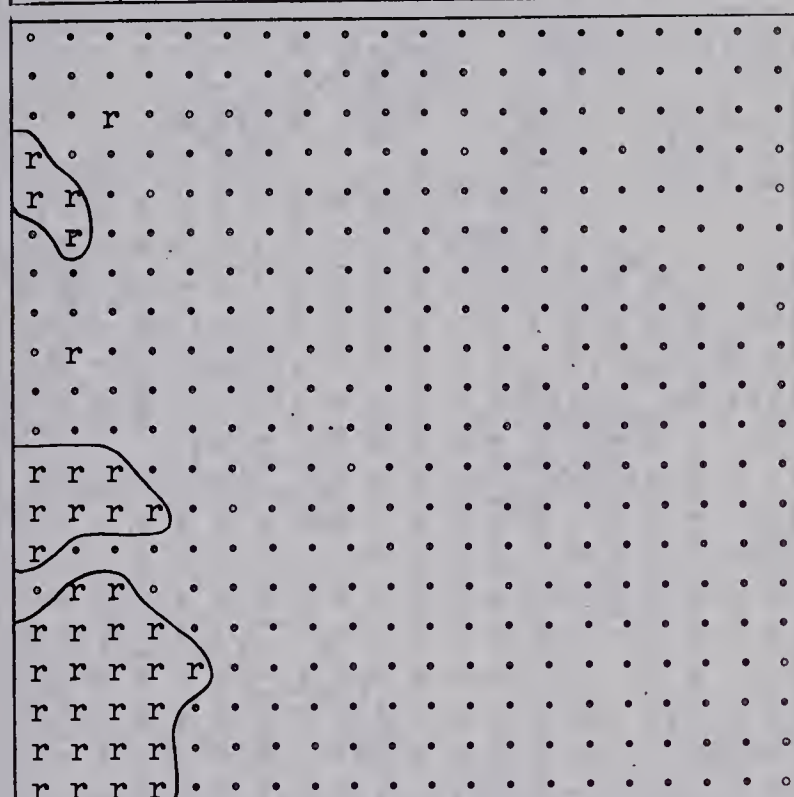


FIGURE 154

Hieracium albertinum

55-J-I

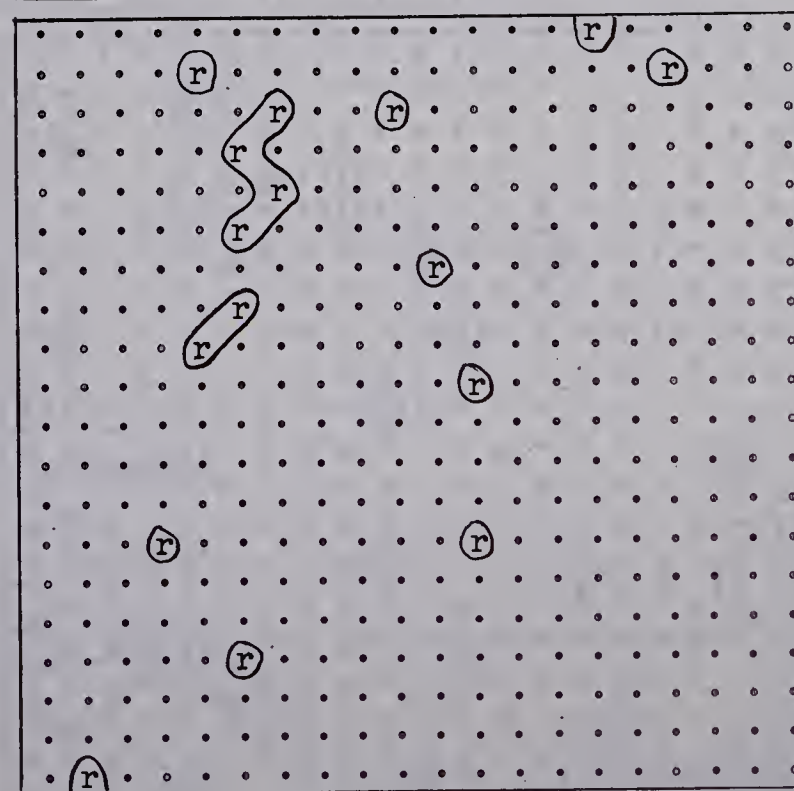


FIGURE 155

Pleurozium schreberi

55-J-I

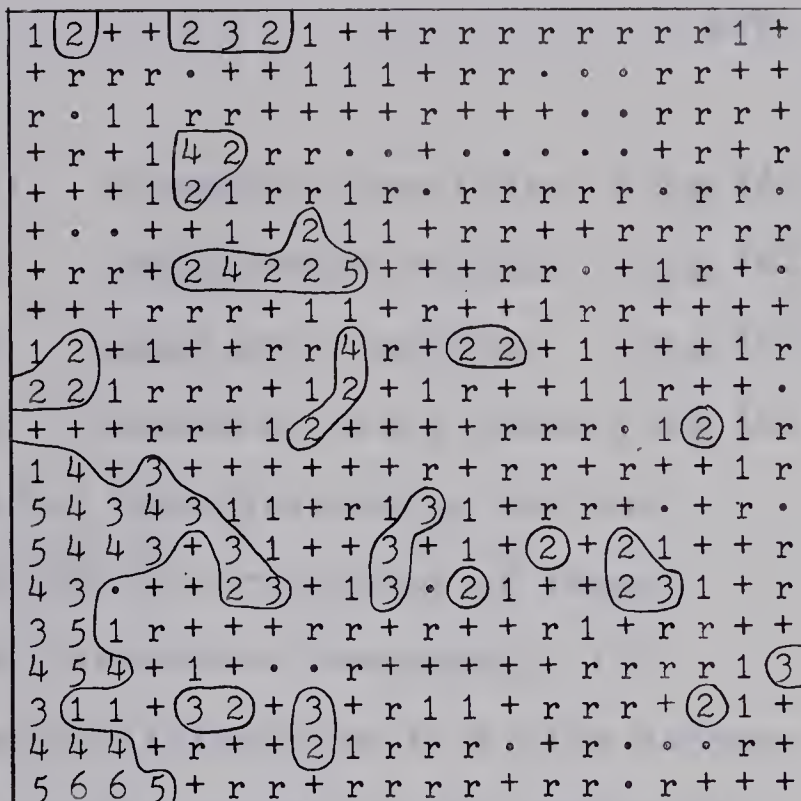


FIGURE 156

Ptilium crista-castrensis

55-J-I

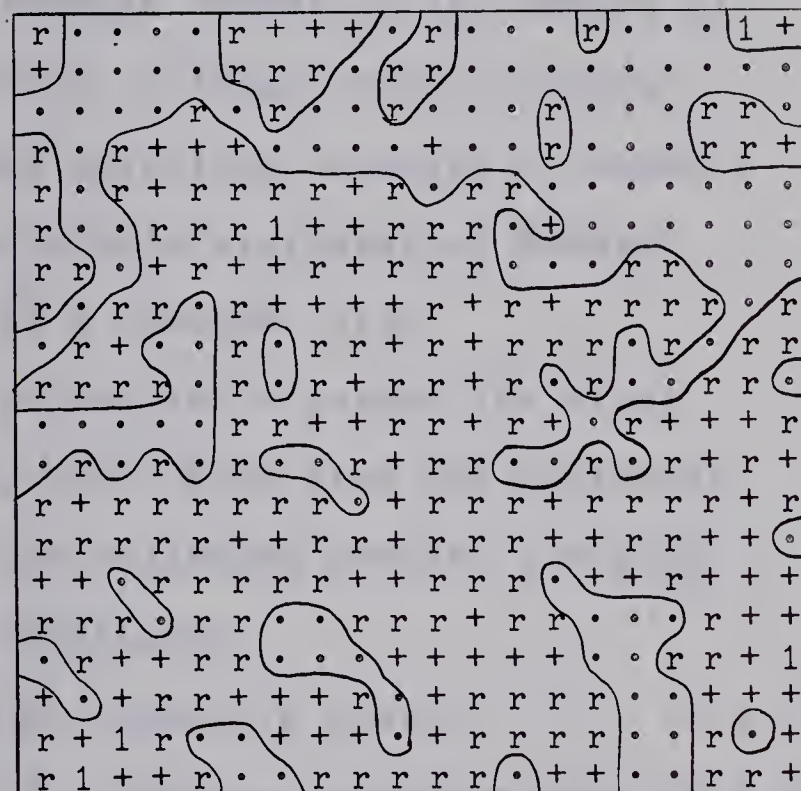
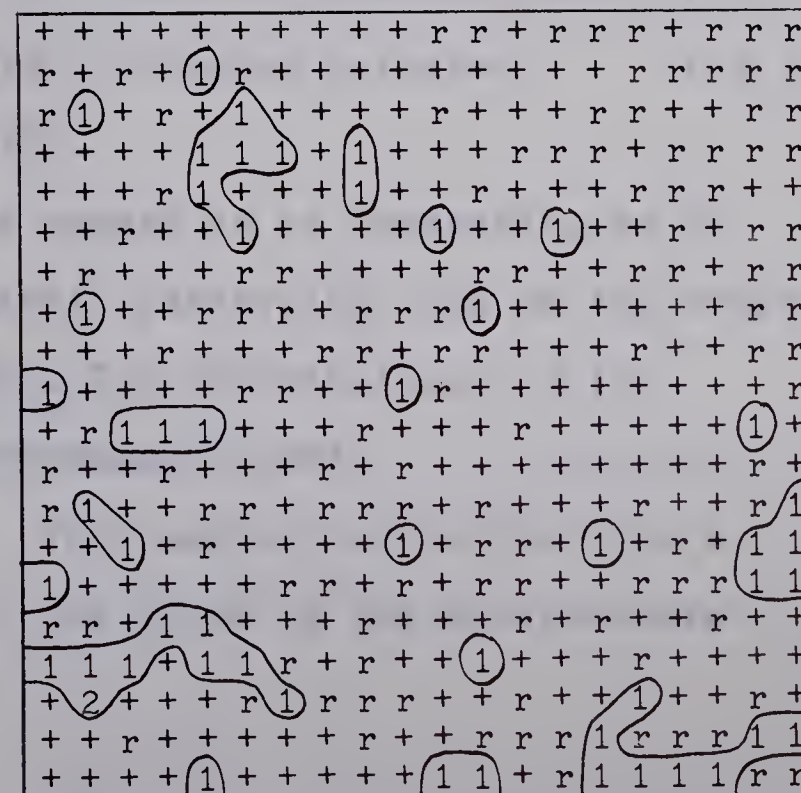


FIGURE 157

Peltigera spp.

55-J-I



Arnica cordifolia (Fig.152) *Chimaphila unbellata* (Fig.163)
Aster conspicuus (Fig.159) *Corallorhiza trifida* (Fig.162)
Calypso bulbosa (Fig.160) *Ledum groenlandicum* (Fig.161)
Castilleja miniata (Fig.158) *Vaccinium vitis-idaea* (Fig.165)

are more widely distributed but show preference for the moister areas. By comparing the distributions of these latter species, plus that of *Shepherdia canadensis*, it would appear that another moist strip about 40 m wide extends across the plot from the northwest corner to the centre of the south side. The occurrence of these "moist" indicator species outside the zones described as moist is usually due to the presence of a favourable microhabitat beneath a shrub, on the north side of a hummock, etc..

The xeric sites occur in two bands across the study plot: the southwest corner, and a band from the northwest to the southeast corners. The following species are good indicators of dry, exposed conditions:

Achillea millefolium (Fig.170) *Agoseris glauca* (Fig.175)
Agoseris aurantiaca (Fig.175) *Senecio cymbalarioides* (Fig.173)
Antennaria racemosa (Fig.168) *Trisetum spicatum* (Fig.174)
Solidago decumbens (Fig.167)

The above noted species appear to be responding to a different scale of environmental patterning than do the other species present in the stand. The distributions of the former species do not clearly reveal a pattern which I can interpret. This may be due to the size of the quadrat used relative to the scale of the environmental

FIGURE 158

Castilleja miniata

55-J-I

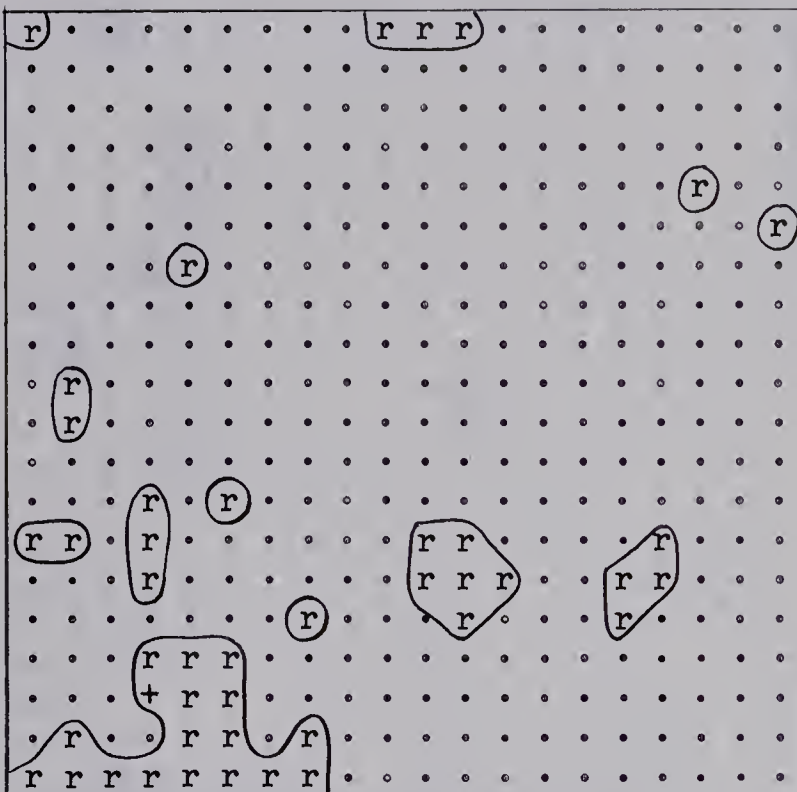


FIGURE 159

Aster conspicuus

55-J-I

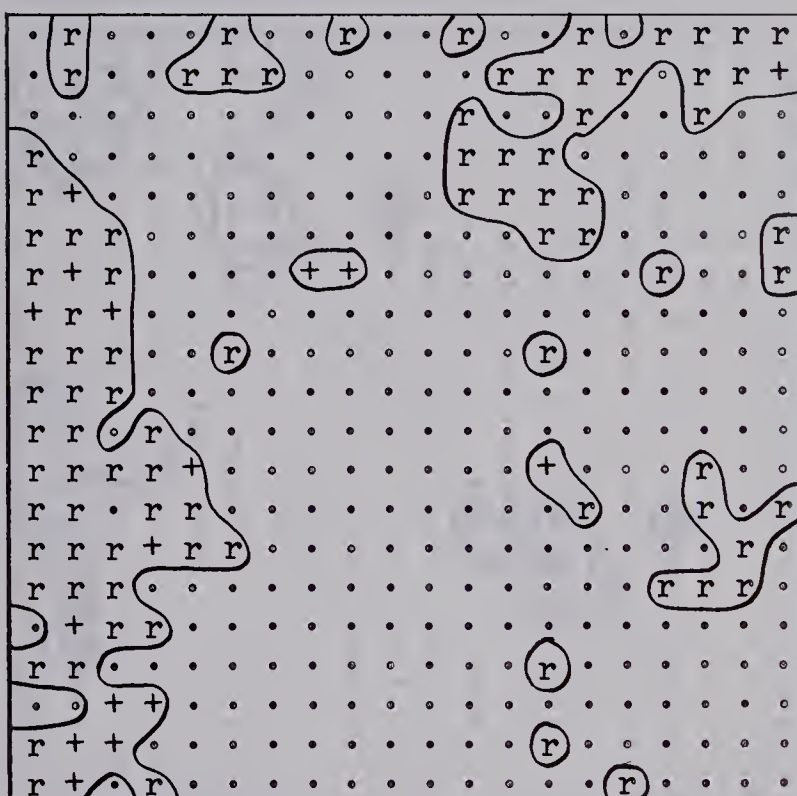


FIGURE 160

Calypso bulbosa

55-J-I

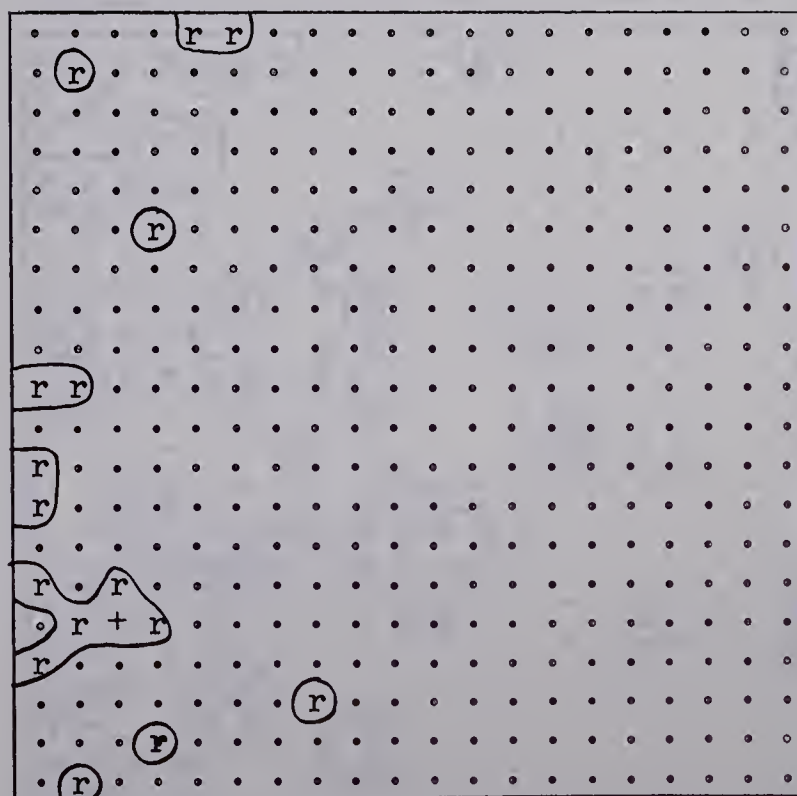


FIGURE 161

Ledum groenlandicum

55-J-I

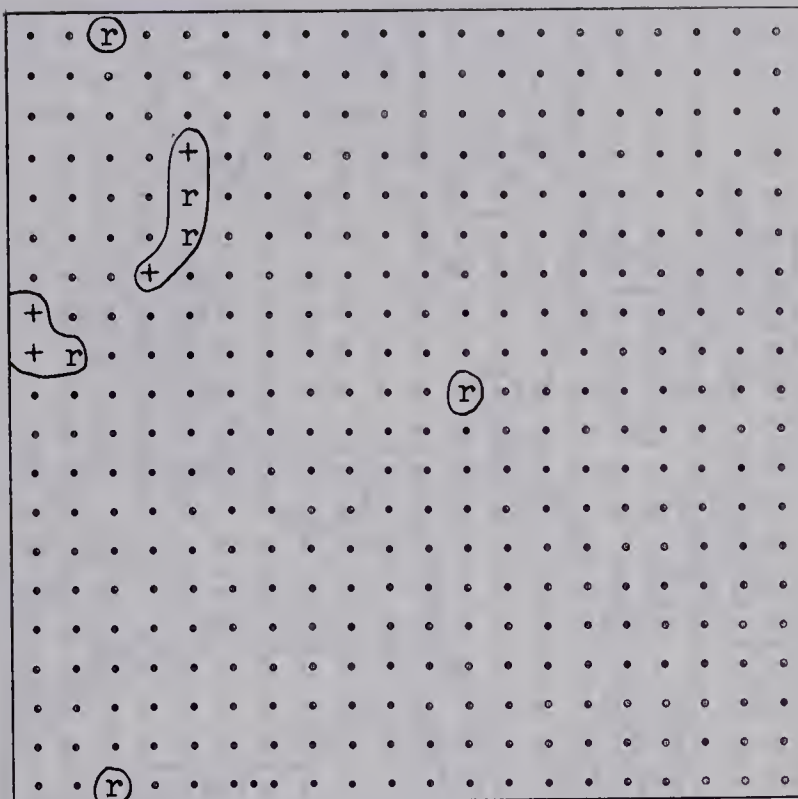


FIGURE 162

Corallorhiza trifida

55-J-I

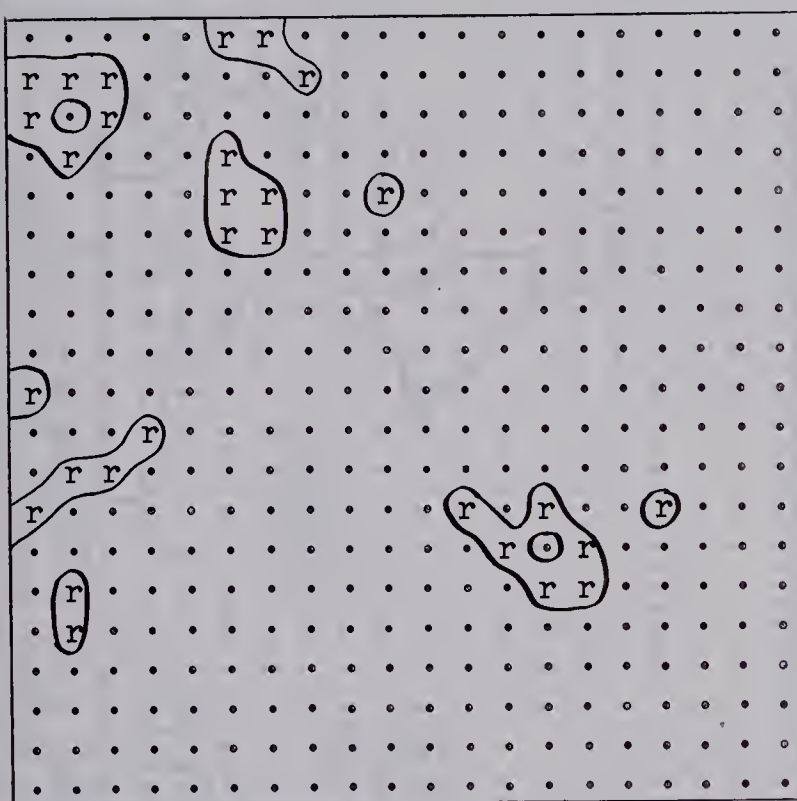


FIGURE 163

Chimaphila umbellata

55-J-I

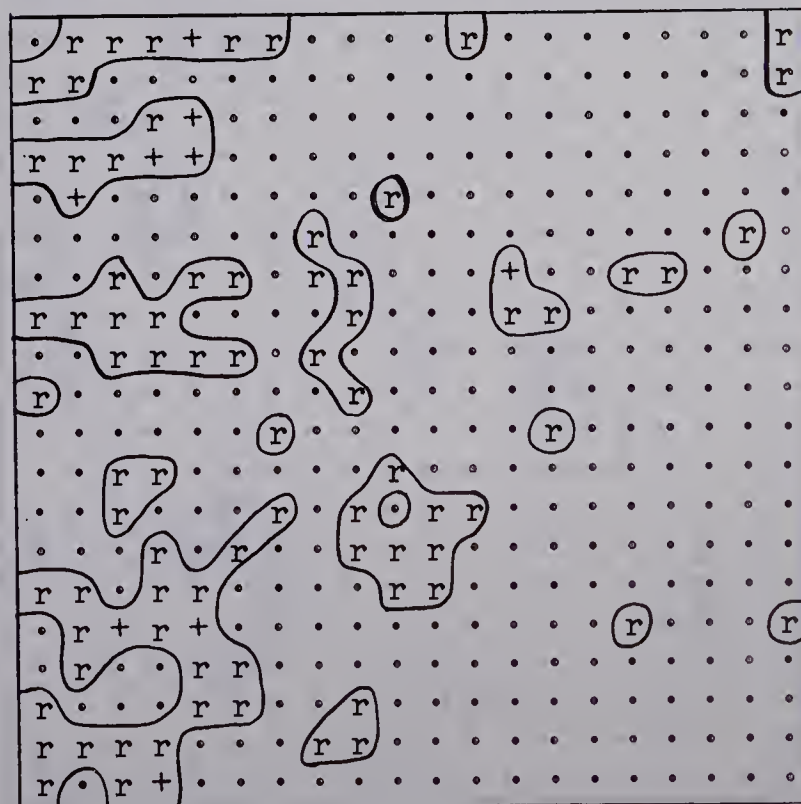


FIGURE 164

Vaccinium caespitosum

55-J-I

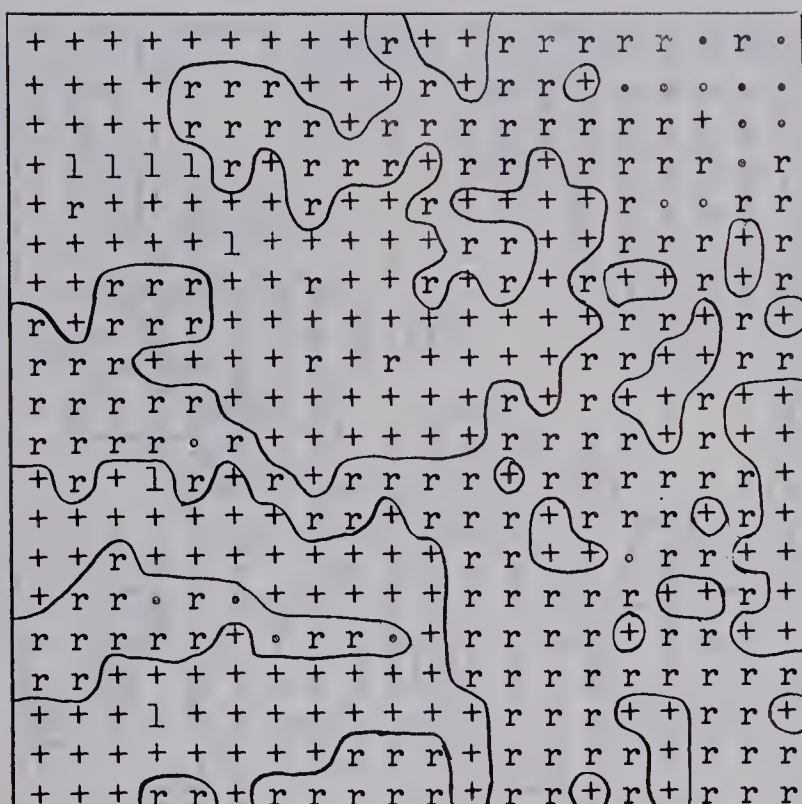


FIGURE 165

Vaccinium vitis-idaea

55-J-I

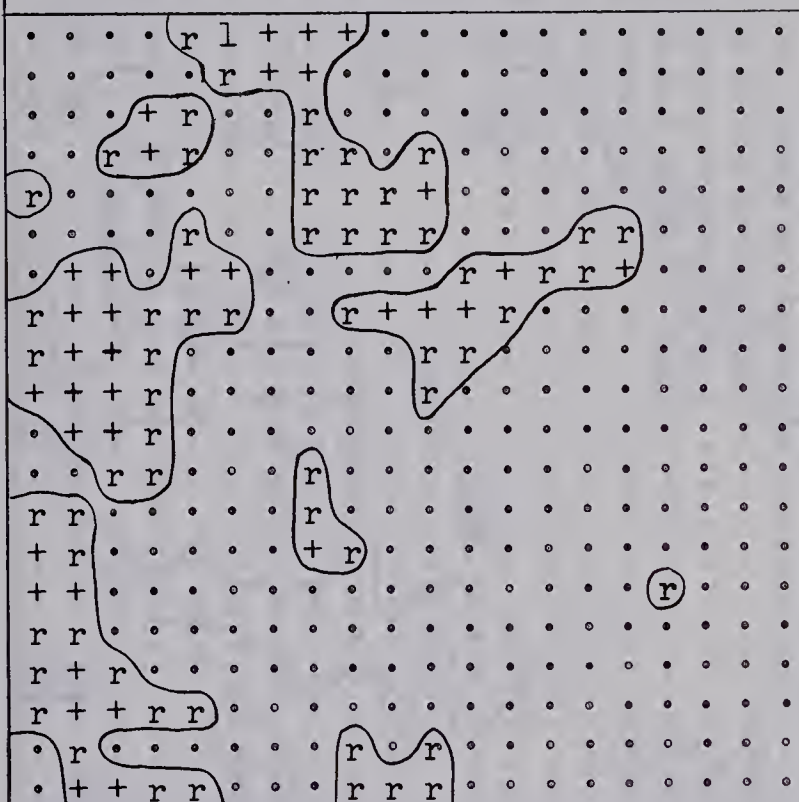


FIGURE 166

Menziesia glabella

55-J-I

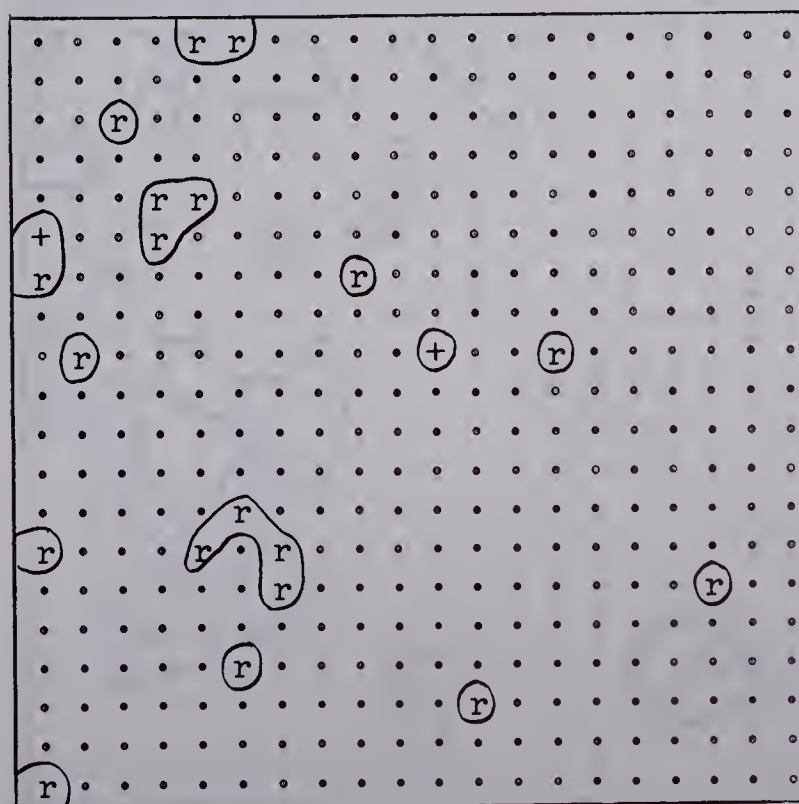


FIGURE 167

Solidago decumbens

55-J-I

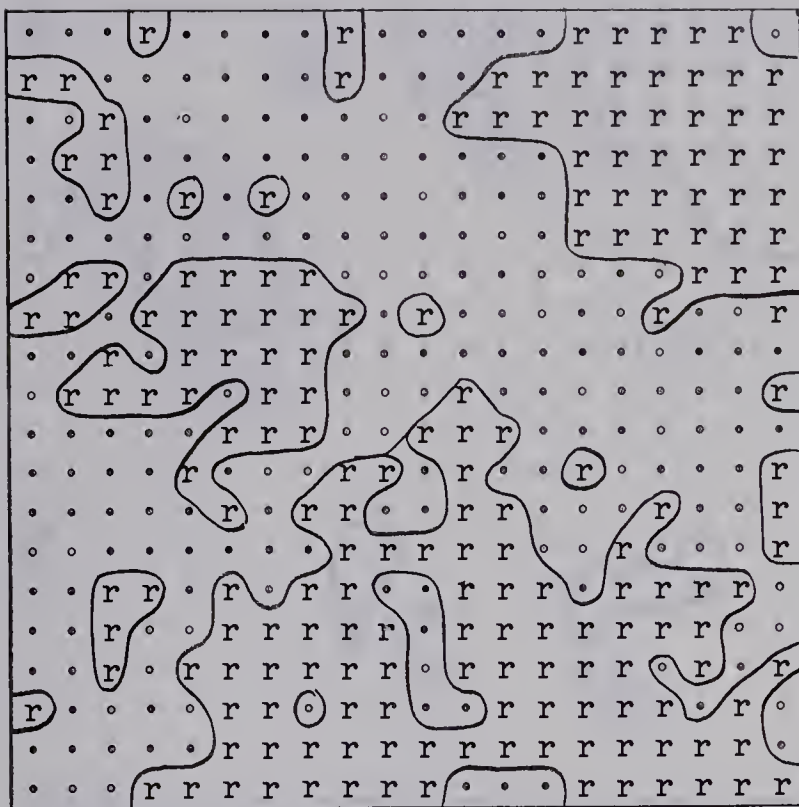


FIGURE 168

Antennaria racemosa

55-J-I

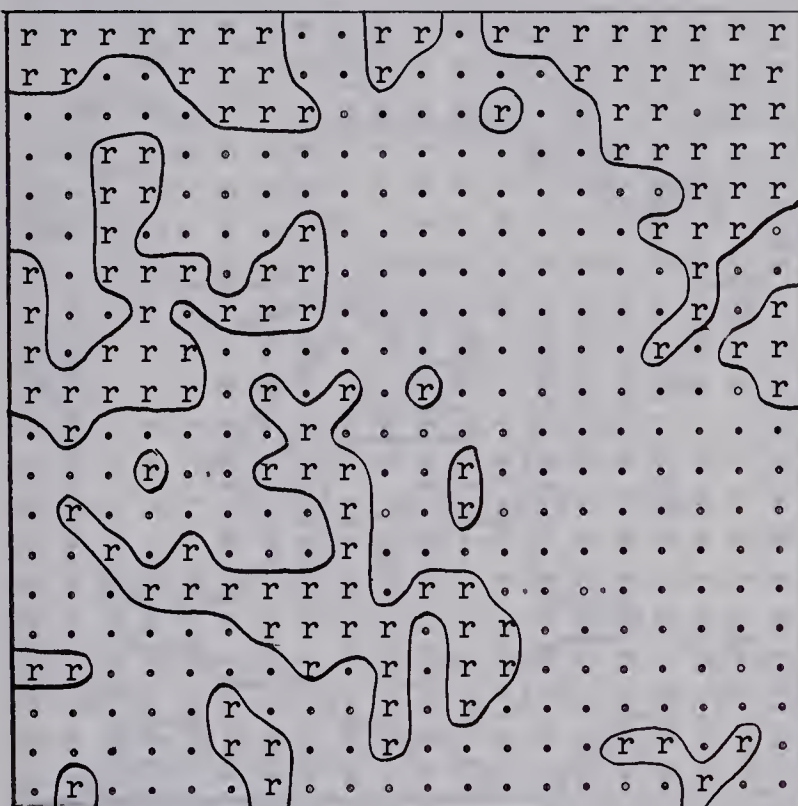


FIGURE 169

Solidago multiradiata

55-J-I

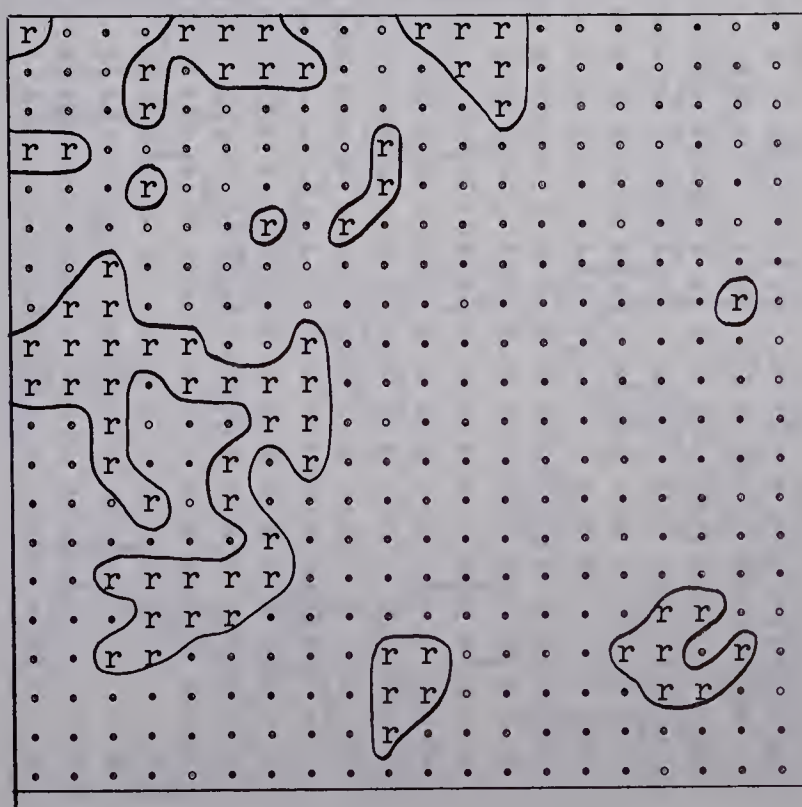


FIGURE 170

Achillea millefolium

55-J-I

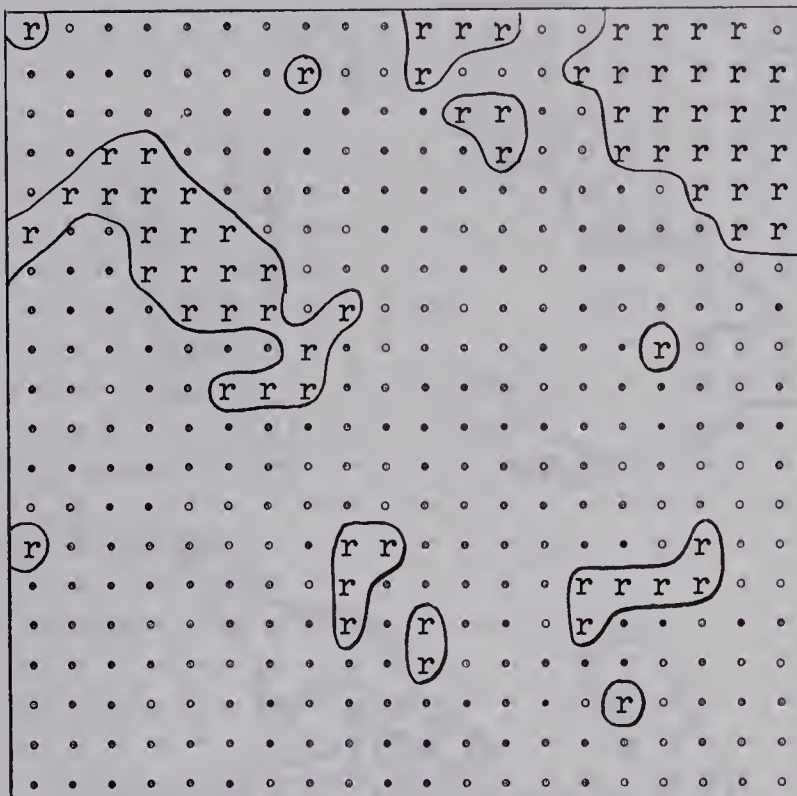


FIGURE 171

Elymus innovatus

55-J-I

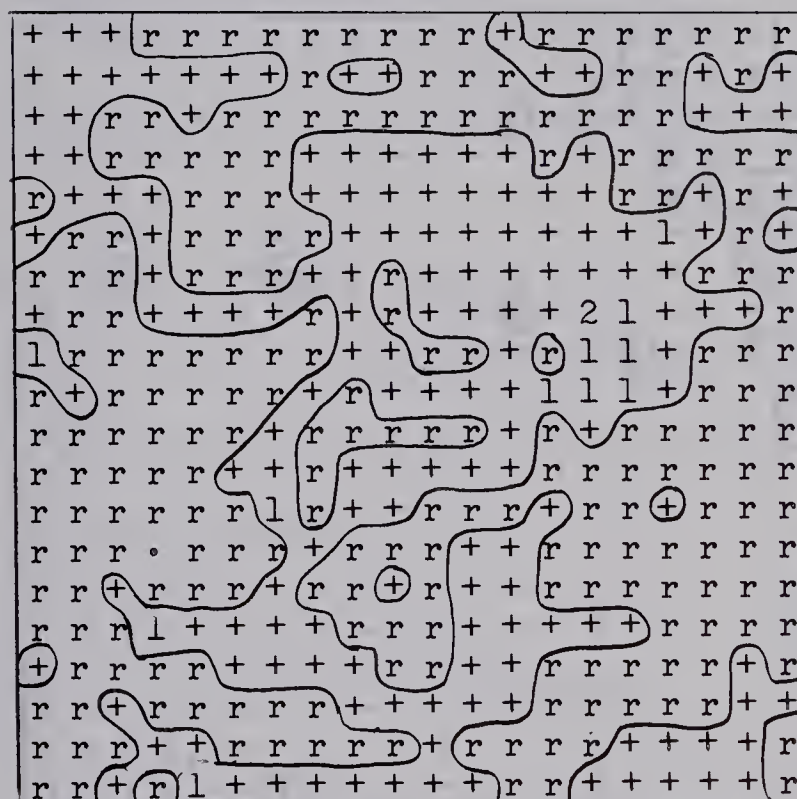
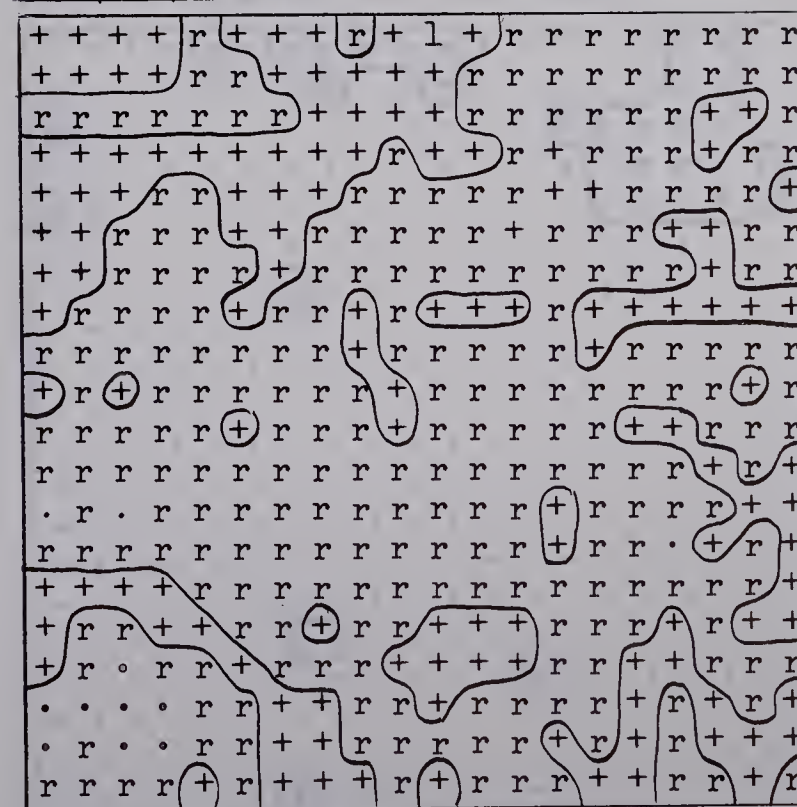


FIGURE 172

Melampyrum lineare

55-J-I





1870
1871
1872



1873
1874
1875



1876
1877
1878

FIGURE 173

Senecio cymbalaroides

55-J-I

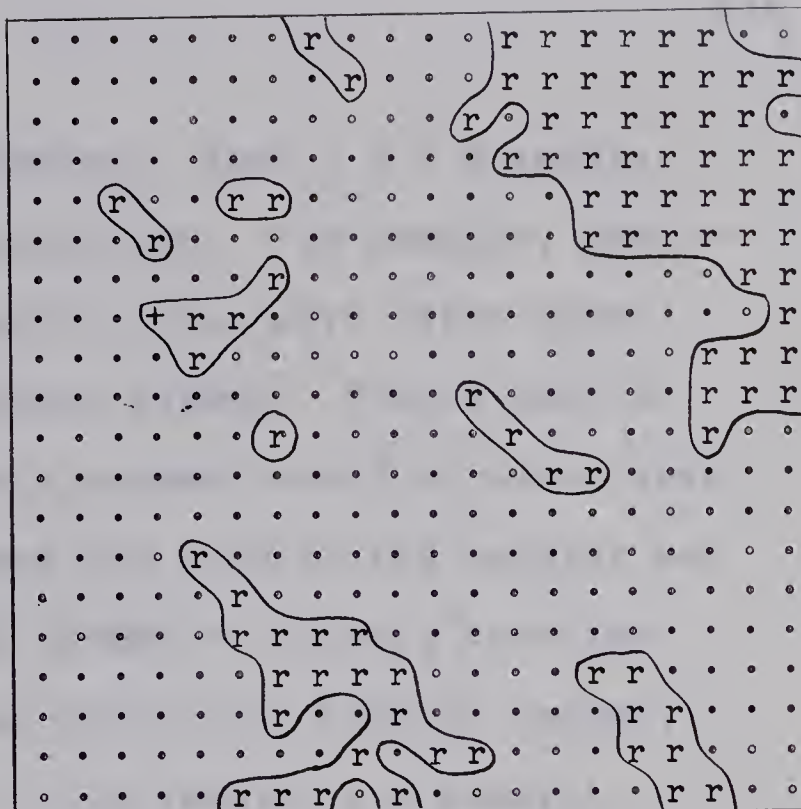


FIGURE 174

Trisetum spicatum

55-J-I

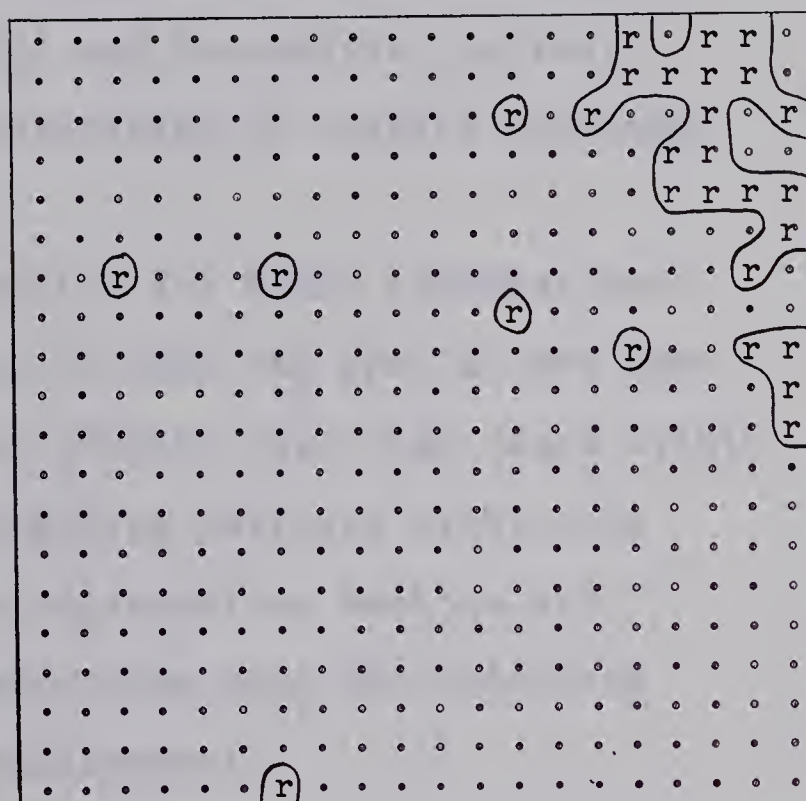
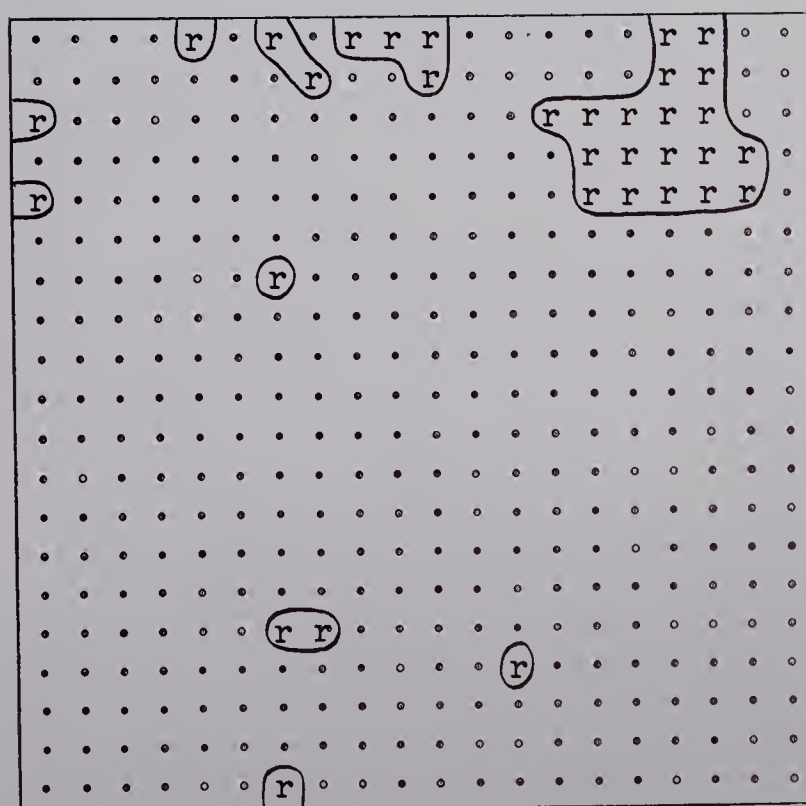


FIGURE 175

Agoseris spp.

55-J-I



factors controlling these species. Each 5 x 5 m quadrat included much microhabitat variation. For example, shadier and therefore cooler and moister sites were often found beneath *Shepherdia* and *Juniperus* clumps. Plants such as *Hylocomium splendens* or *Pyrola secunda* would be associated with these clumps, but because the area of the quadrat was much larger than that of the clumps of shrubs, both the moister habitat and the often more xeric habitat beyond, were included in one sample. The result is a quadrat represented by both mesophytic and xerophytic species. This only confuses the interpretation of species distribution patterns.

Another possible explanation for these somewhat perplexing distribution patterns is that the species may have a range of habitat tolerances greater than that found within the stand. Thus their distribution patterns within the stand would depend more upon reproductive methods and dispersal mechanisms and chance than upon the selective pressures of the immediate environment.

FIGURE 176

Gentianella amarella

55-J-I

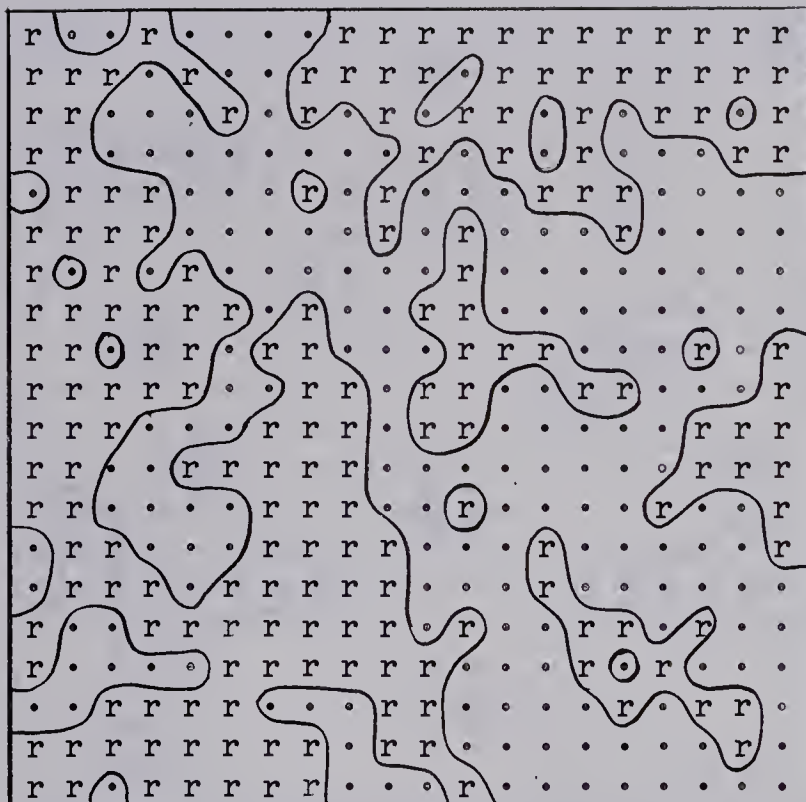


FIGURE 177

Aster ciliolatus

55-J-I

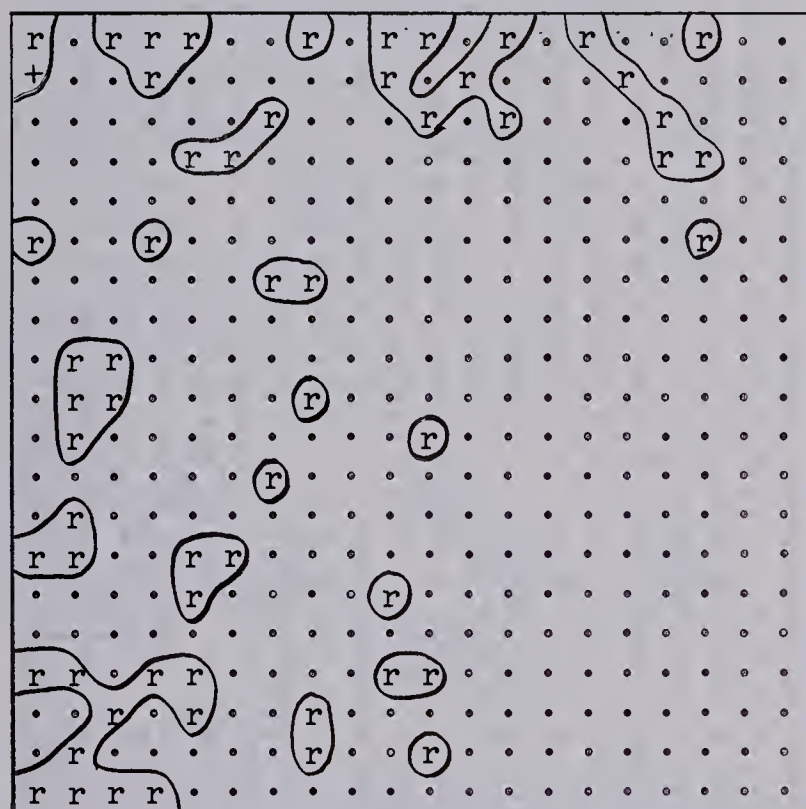


FIGURE 178

Cornus canadensis

55-J-I

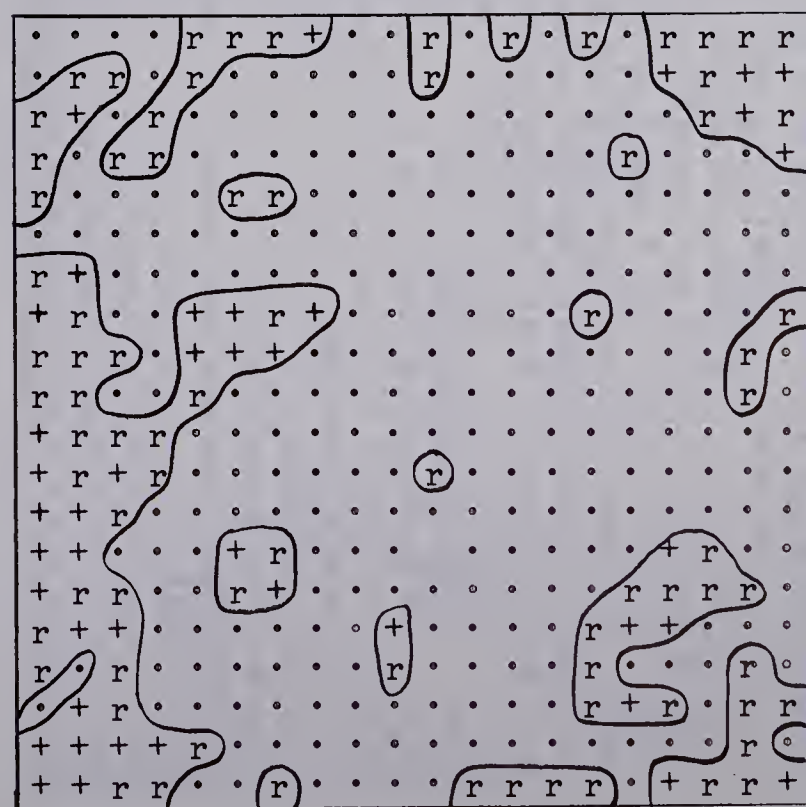


FIGURE 179

Goodyera oblongifolia

55-J-I

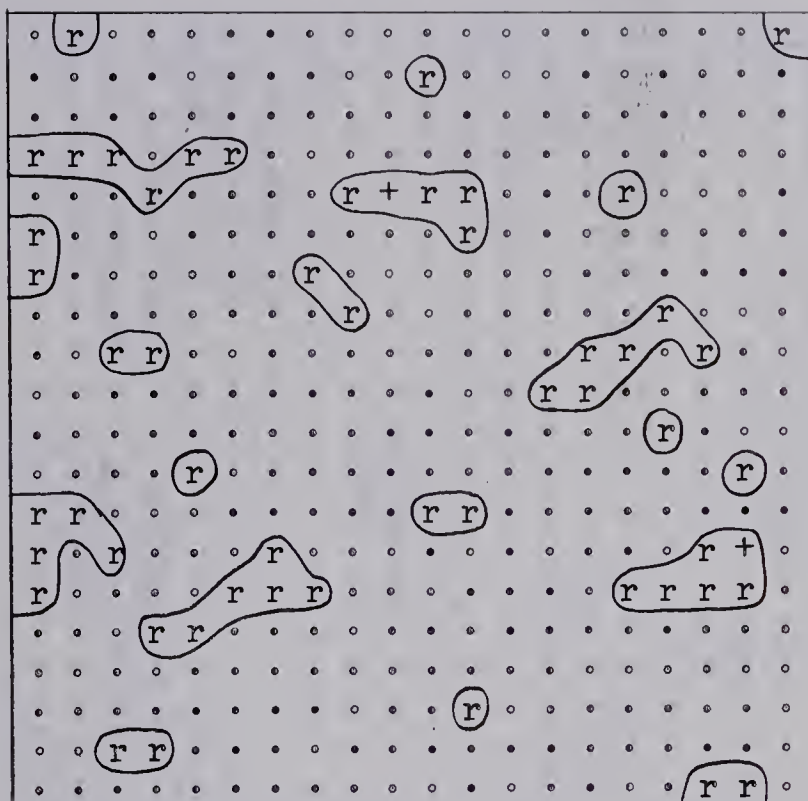


FIGURE 180

Fragaria virginiana

55-J-I

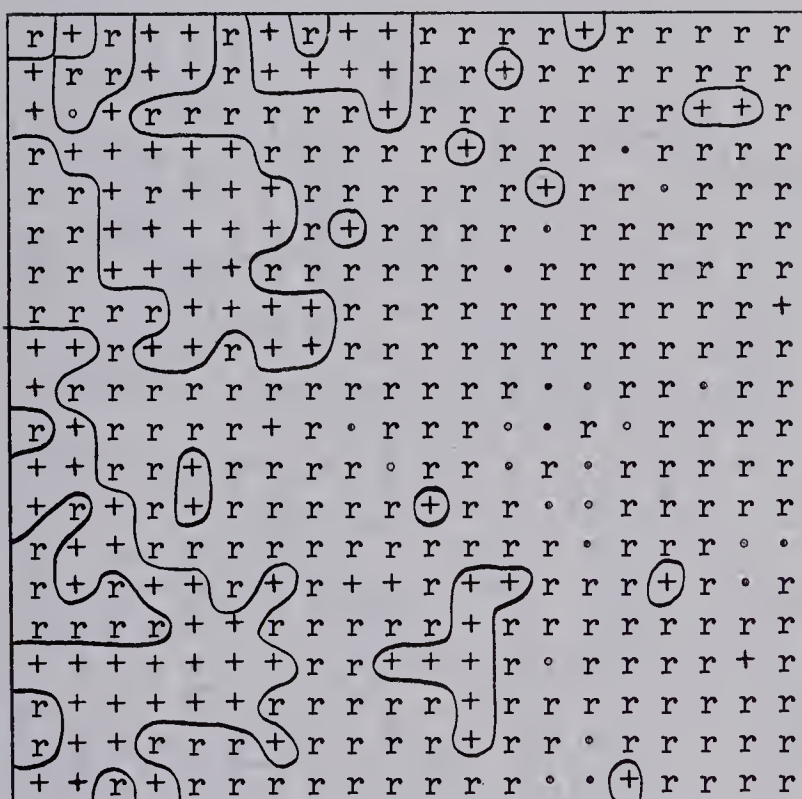


FIGURE 181

Rosa acicularis

55-J-I

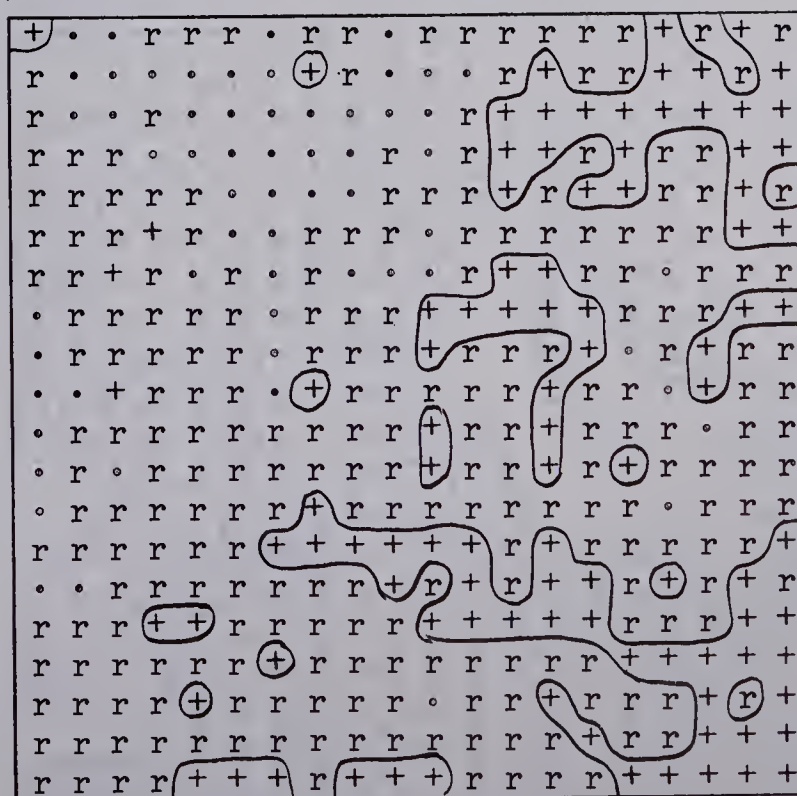


FIGURE 182

Linnaea borealis

55-J-I

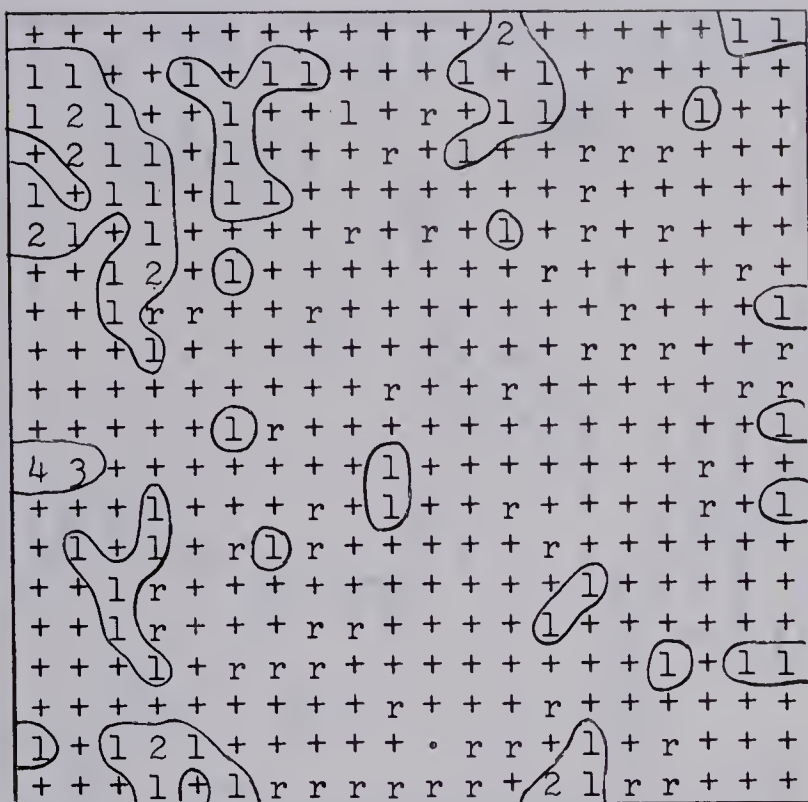


FIGURE 183

Arctostaphylos uva-ursi

55-J-I

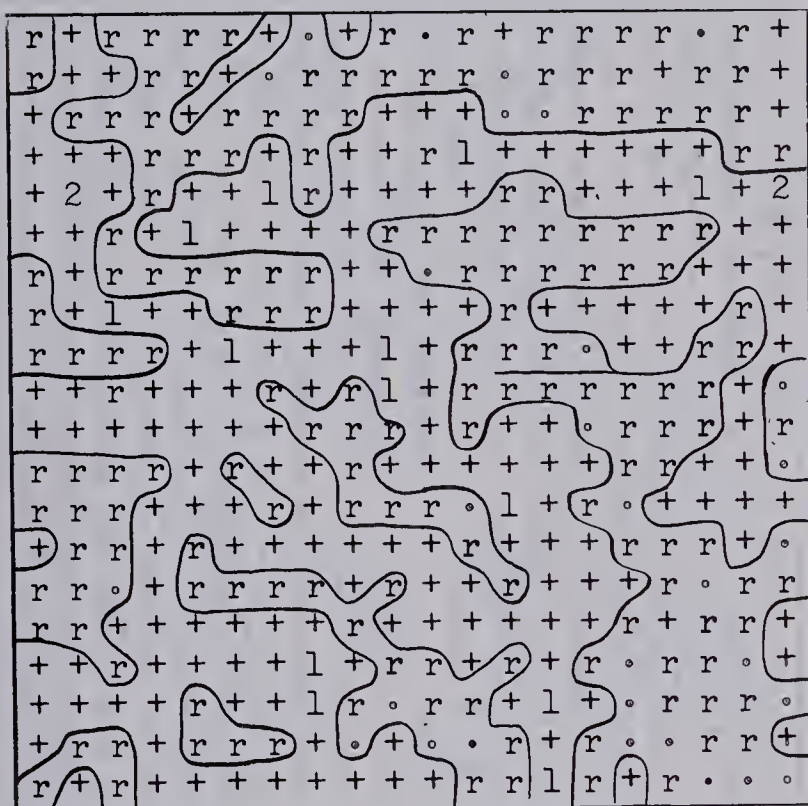


FIGURE 184

Antennaria neglecta

55-J-I

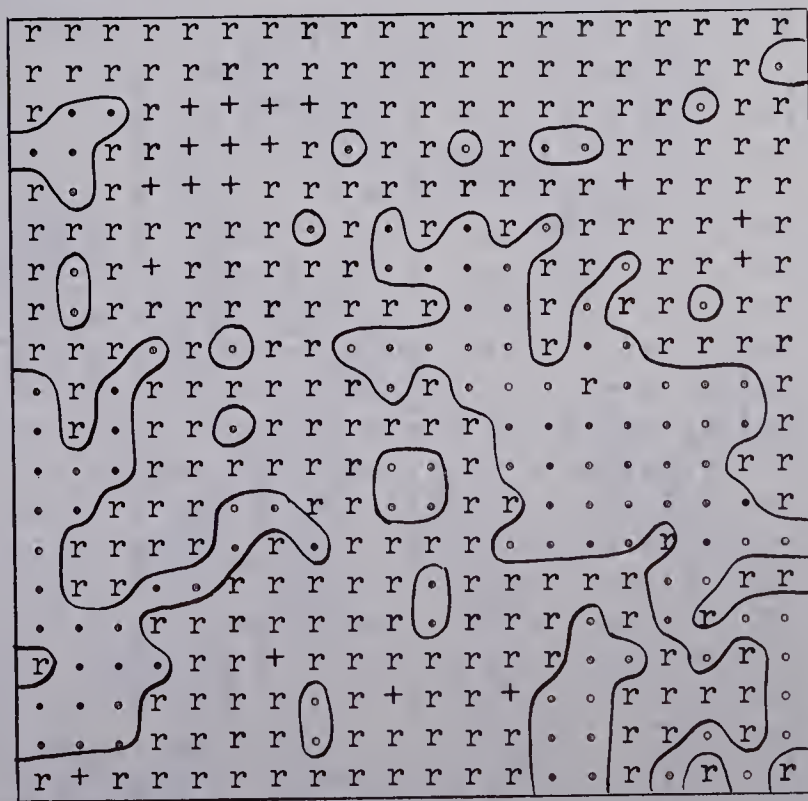


FIGURE 185

Vaccinium scoparium

55-J-I

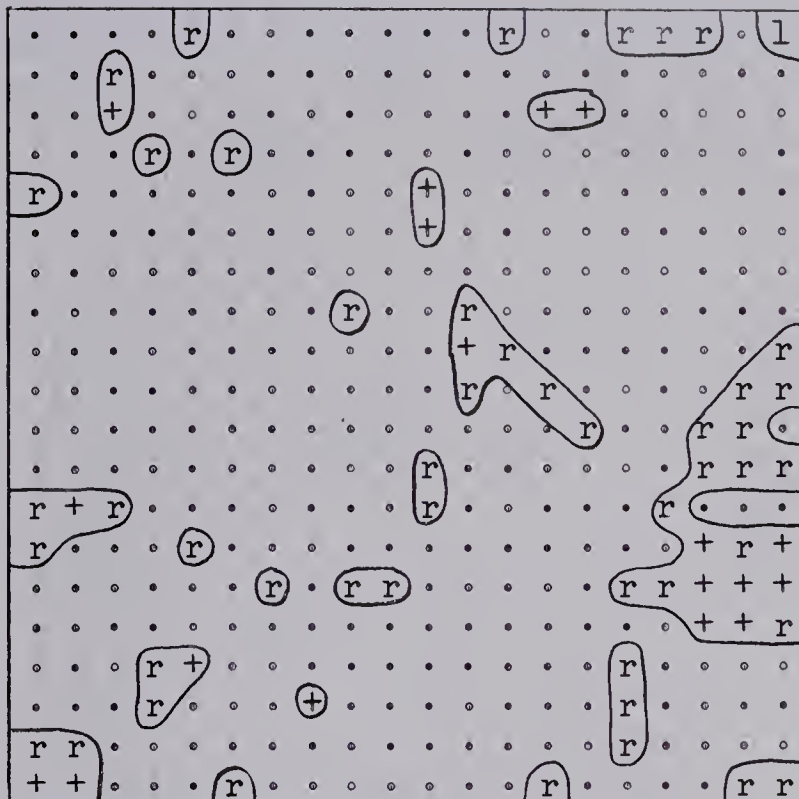


FIGURE 186

Shepherdia canadensis

55-J-I

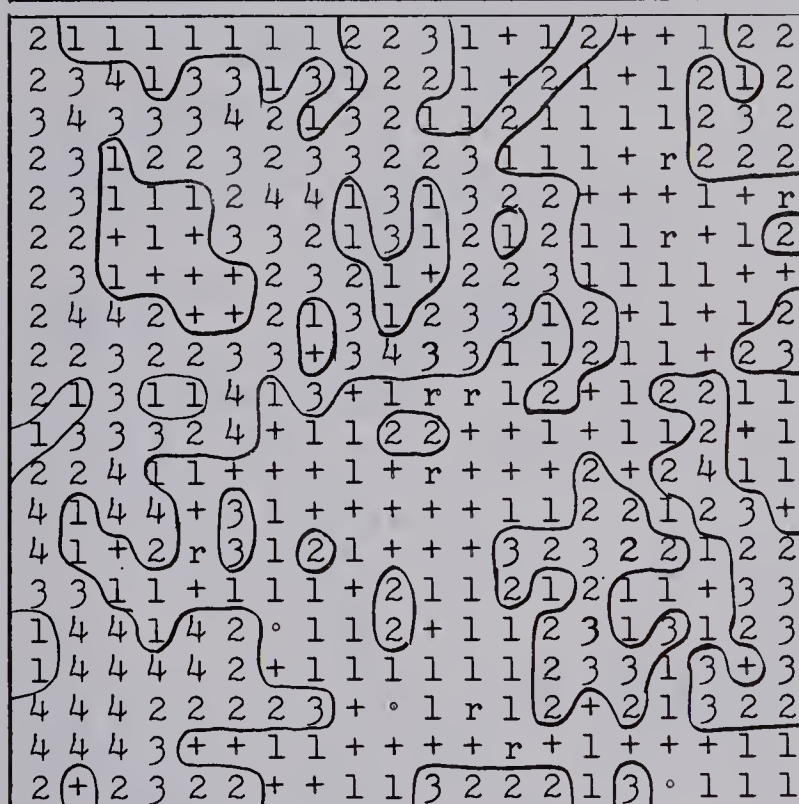
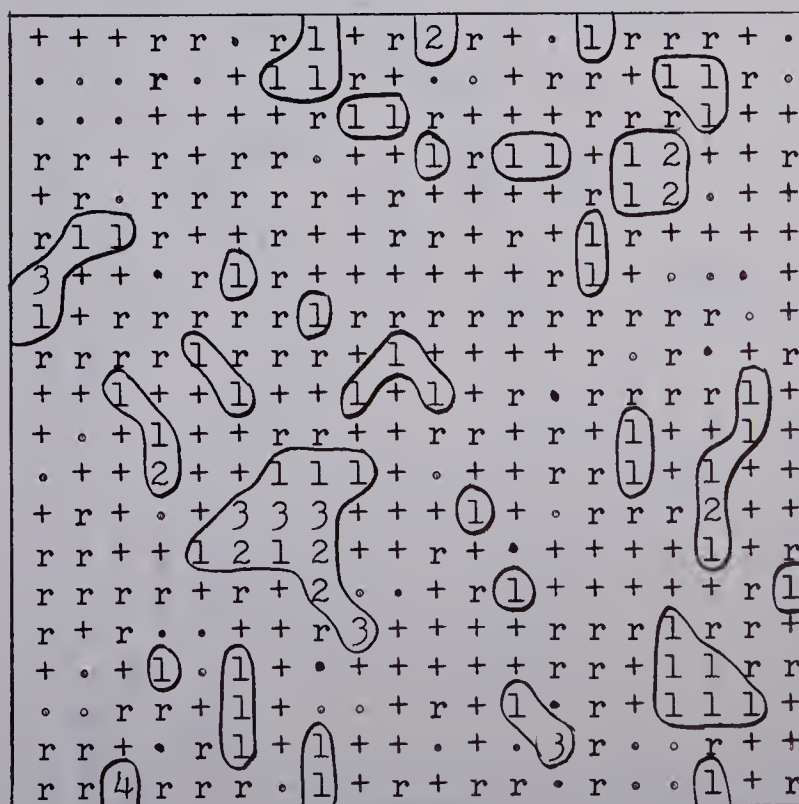


FIGURE 187

Juniperus communis

55-J-I



[Faint, illegible text, likely bleed-through from the reverse side of the page.]

[Faint, illegible text, likely bleed-through from the reverse side of the page.]

FIGURE 188

Pyrola virens

55-J-I

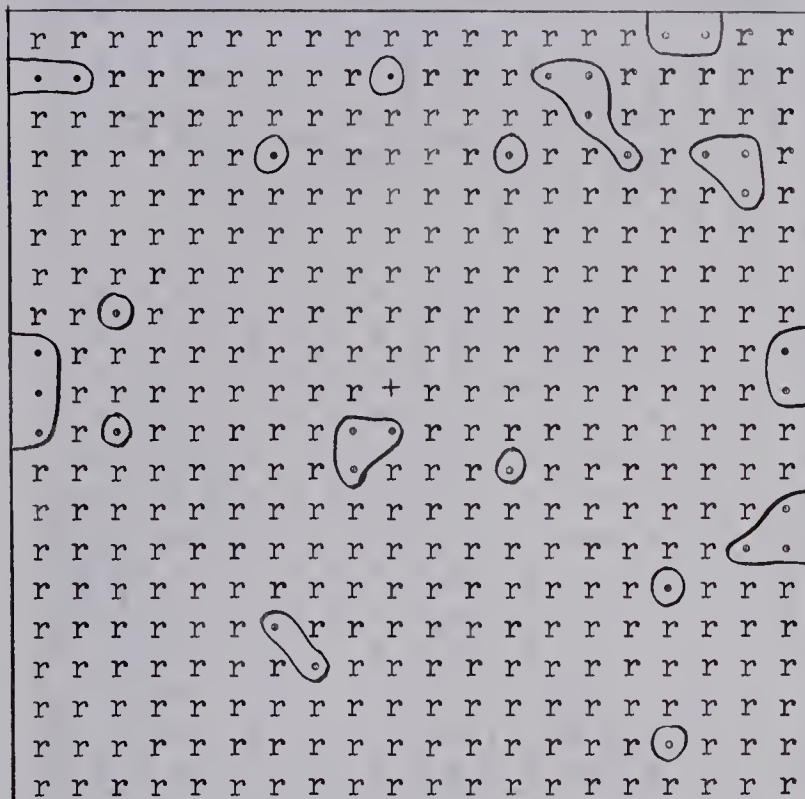


FIGURE 189

Pyrola secunda

55-J-I

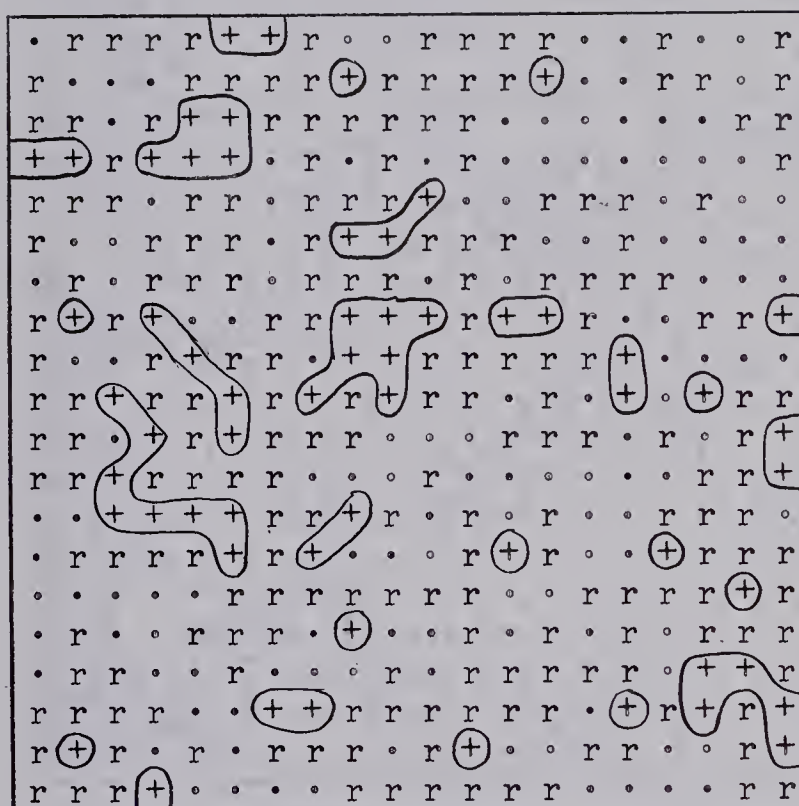


FIGURE 190

Salix spp.

55-J-I

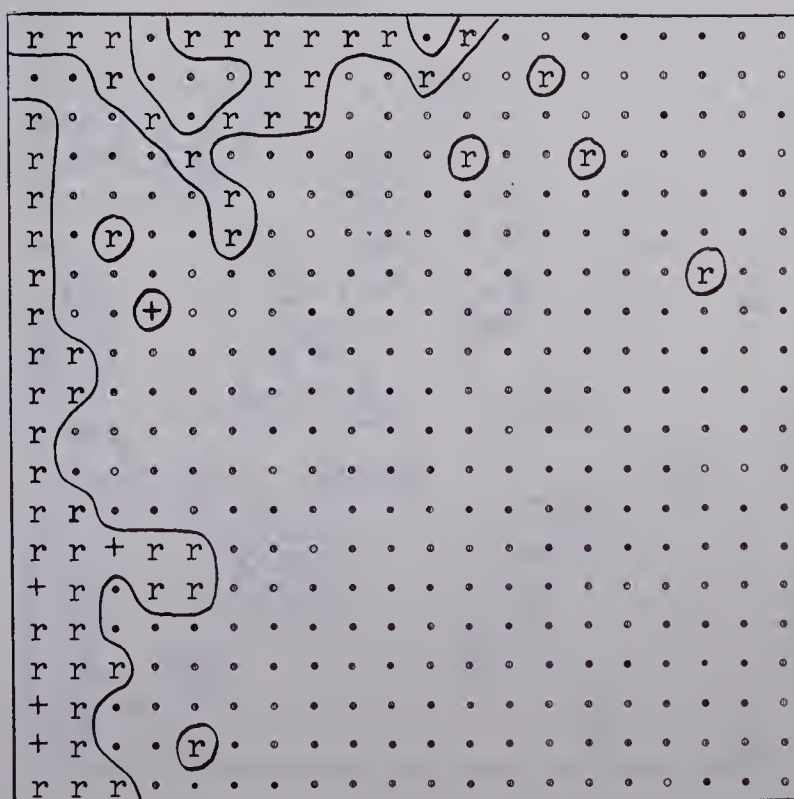


FIGURE 191

Polytrichum juniperinum

55-J-I

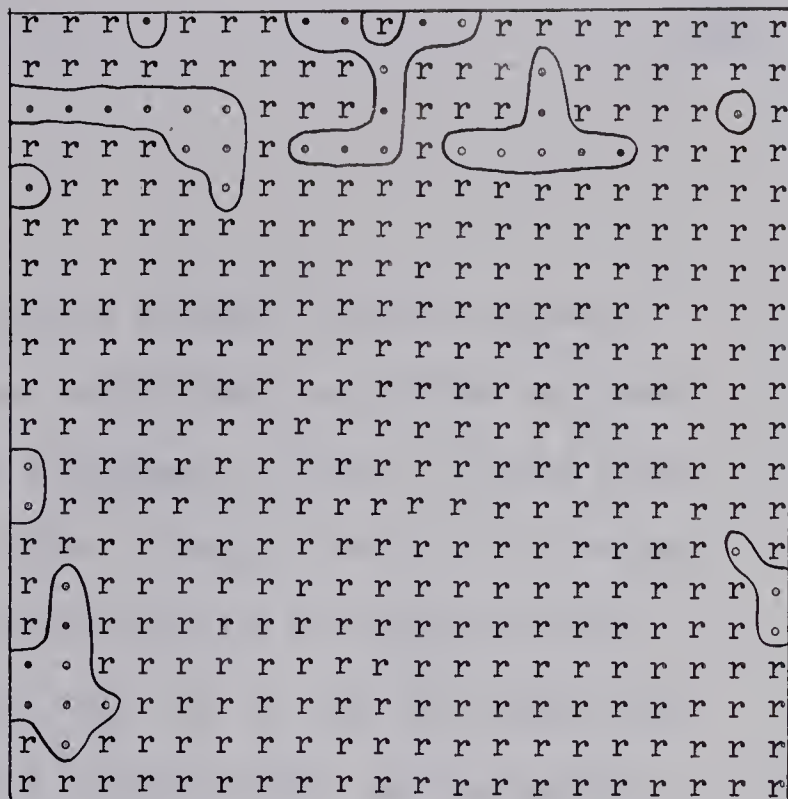


FIGURE 192

Dicranum polysetum

55-J-I

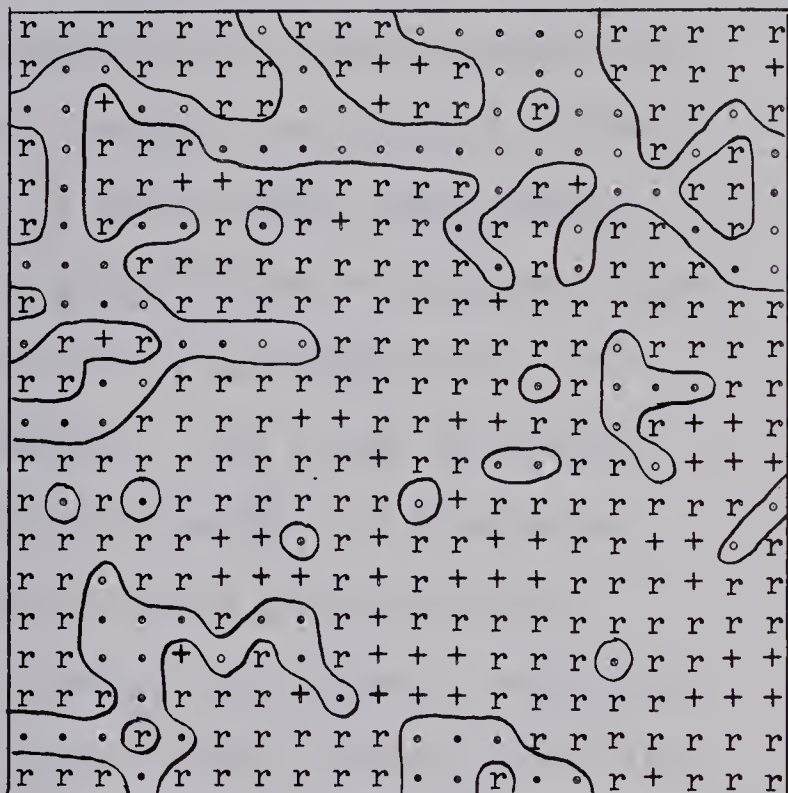
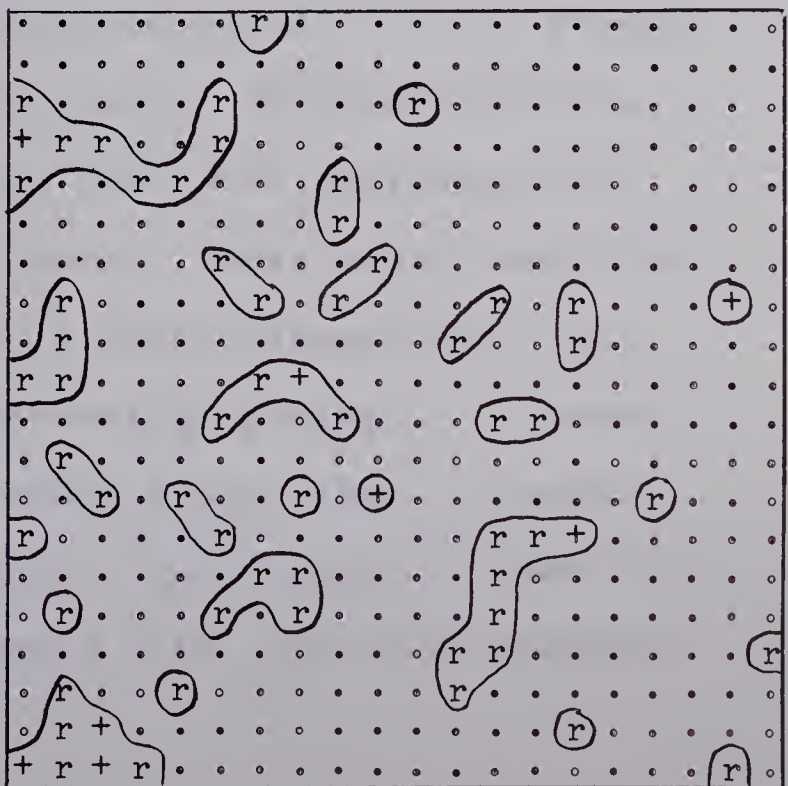


FIGURE 193

Hylocomium splendens

55-J-I



Handwritten text in the top left section, appearing to be a list or series of notes.

Handwritten text in the middle left section, continuing the list or notes.

Handwritten text in the bottom left section, possibly concluding the list or notes.

Handwritten text in the top right section, possibly a title or header.

Handwritten text in the middle right section, possibly a title or header.

Handwritten text in the bottom right section, possibly a title or header.

5. 24-J-I: TREE STRATUM

The tree stratum of this stand consists almost exclusively of *Pinus contorta*, with the exception of four *Picea mariana* located in the southwest corner of the area. This latter site is on the slope joining the two terraces. Fig. 194 shows the pine to be definitely contagiously distributed. By comparison with Fig. 16 it can be seen that the greatest area of contagion corresponds approximately to the location of the major dune in the north centre of the stand. The large openings roughly correspond to the flatter areas where the soil is very coarse and stoney.

The patterning of the tree distribution appears to be a predictable outcome of the history and habitats of the stand and not a chance phenomenon. The stand occurs at the bottom of the low, broad, relatively dry Athabasca River valley. This area receives less precipitation (Fig. 7) than other areas of equal and higher elevation. This area is not unique in Jasper--many similar areas in different stages of development can be seen in the bottom of the Athabasca Valley, for example, the Prairie de la Vache and the area immediately above the confluence of the Sunwapta and Athabasca rivers. These areas show that the pine becomes established in small clumps then very slowly invades the large intervening openings. If stand 24-J-I is representative of these areas, then I predict from the study of this stand that the clumps of pines in these other areas are associated with stone-free patches

FIGURE 194

24-J-I

Pinus contorta
trees

1= 1-3 individuals
2= 4-5 individuals
3= more than 5
individuals.

202

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 2 | | 3 | 3 | 2 | 2 | 1 | 3 | 1 | 3 | 3 | 1 | 3 | 2 | 1 | 1 | 2 | 2 |
| 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | | 1 | 2 | 3 | 3 | 3 | 3 | 3 | 1 | | 3 | 3 |
| 1 | 3 | 2 | 1 | | | 1 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 3 | 2 | 1 | 1 | 1 | 3 |
| 2 | 3 | 3 | 3 | 1 | 2 | 1 | 3 | 3 | 3 | 1 | 3 | 1 | 1 | 3 | 2 | 1 | 1 | 1 | |
| 3 | 1 | 3 | 1 | 3 | 3 | 2 | 3 | 2 | 1 | 1 | 3 | 2 | 1 | 3 | 2 | | 1 | 1 | 3 |
| 3 | 3 | 3 | 3 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 3 | 3 | 3 |
| 3 | 3 | 3 | 3 | 3 | 2 | 1 | 1 | 1 | 3 | 2 | 1 | 1 | | 1 | 2 | 3 | 2 | 1 | 1 |
| 2 | 2 | 3 | 1 | 3 | | 1 | 1 | | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | | 1 |
| 1 | 2 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 1 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 3 | 1 | 1 | 2 | 2 | 3 | 3 | 3 | 1 | 2 |
| 2 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 1 | 1 | 1 | 3 | 3 | 3 | 3 | 1 | 1 |
| 1 | 3 | 3 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 1 | 3 | 2 | 3 | 3 | 3 | 1 | 1 |
| 1 | | 1 | 1 | | 3 | 3 | 3 | 3 | 3 | 3 | | 1 | 1 | 3 | 3 | 1 | 1 | 1 | 1 |
| | 1 | 1 | | 1 | 2 | 3 | 3 | 3 | 3 | 3 | 1 | 1 | 2 | 3 | 1 | 3 | 3 | 1 | |
| 2 | | 1 | 1 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | |
| | 1 | 1 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 2 | | 1 | 1 | 2 | 3 |
| 1 | 2 | | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 |
| 1 | | 1 | 3 | 3 | 3 | 3 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 3 | 3 | 3 | 3 | 1 | 3 | 3 | 1 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 3 |
| 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |

FIGURE 195

24-J-I

Pinus contorta
seedlings

numbers = actual
numbers of individuals.

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|----|---|---|---|---|----|---|---|---|---|---|---------|---|---|---|---|
| 5 | | | | | | | | | | | | | | | 1 1 2 1 | | | | |
| | | | | | | | | | | | | | | | 1 2 1 | | | | |
| | | | | | | | | | | | | | | | 1 1 | | | | |
| | | | | | | | | | | | | | | | | | | | |
| 1 | 1 | 1 | | | 2 | 2 | 1 | 2 | | 1 | 2 | | 2 | 2 | 2 | 2 | 2 | 1 | 1 |
| 1 | 4 | 1 | 1 | 2 | 2 | 3 | 4 | 4 | 2 | | 1 | | | | | | | 1 | |
| | | | | | | | | | | | | | | | 1 1 2 | | | | |
| 7 | 3 | | | | 3 | 4 | | | | | 1 | | 1 | 4 | | | | | |
| 4 | | | 1 | 1 | 1 | 2 | | 8 | 2 | 4 | 2 | | 1 | 1 | 1 | | | | |
| 5 | 3 | 2 | | 2 | | 1 | | 1 | 2 | | | | | 3 | | | | | |
| 1 | 2 | | | 2 | 2 | | 2 | 1 | | 1 | 2 | | 2 | 2 | 3 | | 2 | | |
| 1 | | | | | | | | 1 | 2 | | 1 | | 1 | 1 | 4 | 1 | 1 | | |
| | 2 | | | | | | 1 | 1 | 1 | | 3 | 2 | 2 | 4 | 6 | | 1 | | |
| 1 | 1 | 2 | | 3 | 1 | 1 | 1 | | 1 | 1 | 1 | 2 | 1 | | 3 | 4 | | 1 | |
| 4 | 5 | 3 | | 12 | | | 1 | | 2 | 3 | 1 | 2 | | 1 | 2 | 1 | 1 | | |
| | 3 | | 1 | | 7 | 3 | 2 | | | 5 | 1 | | | | | | | 5 | |
| 4 | | | | | 1 | 2 | 2 | | 10 | 3 | | | 2 | 1 | | 3 | | | |
| | | | | | | | | | | | | | | | 1 1 2 2 | | | | |

of soil such as would be provided by small dunes or silt-covered islands.

These areas appear to be very prone to fire; from aerial photos they show a complex patterning of fire margins. Old trees in the more open areas of stand 24-J-I show one or more fire scars. Thus it appears that fires completely burn the denser areas of pine occurring on the dunes, but the lack of fuel in the more open areas reduces the fires to relatively ineffectual ground fires (see p. 250). The trees in the open areas may be scarred but many survive the fires, and thus provide ample seed for forest regeneration. The more favourable dune areas permit the establishment of fairly dense clumps of pines. The result is a two-to several-aged pine forest.

Fig. 195, 196, 198, 199 provide strong support for the above interpretation. Firstly, Fig. 195 shows that within the plot there is no difference in seedling germination potential with respect to areas of different tree density or topography. A Chi-square test of geographic homogeneity based upon the comparison of the actual number of quadrats with pine seedlings per block of 16 quadrats and the expected number of such quadrats ($8.25/16$ quadrats) yields a Chi-square of 8.6 which is significant at the 1% level. This indicates that seedling success departs from random expectation in the area.

Fig. 199 shows that the distribution of transgressives in the stand is markedly different from that shown in

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

...the ... of ...

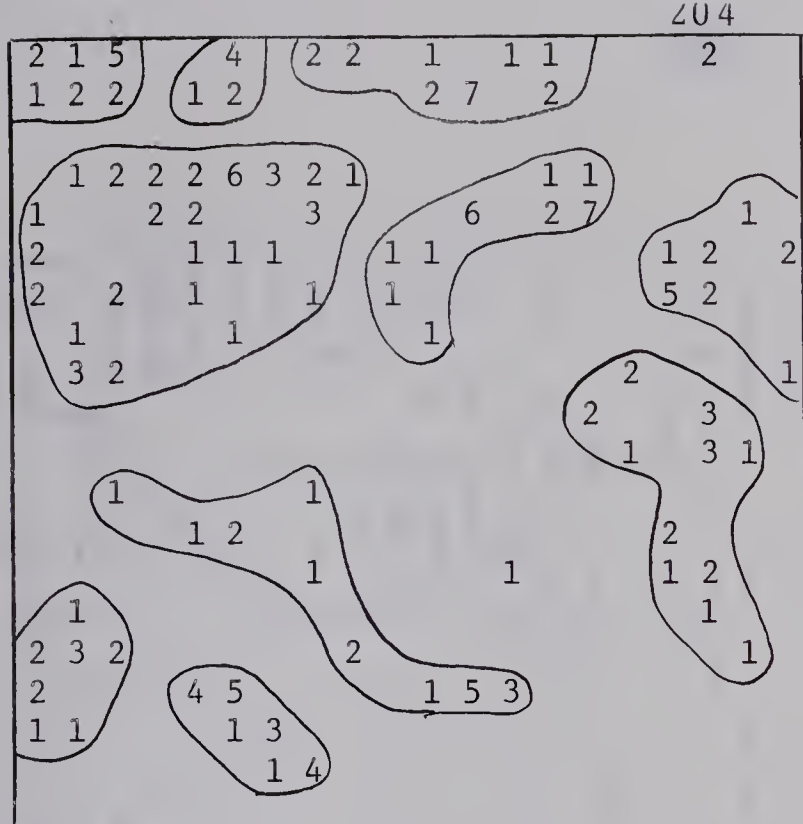
...the ... of ...

...the ... of ...

...the ... of ...

24-J-I

numbers = actual
numbers of individuals.

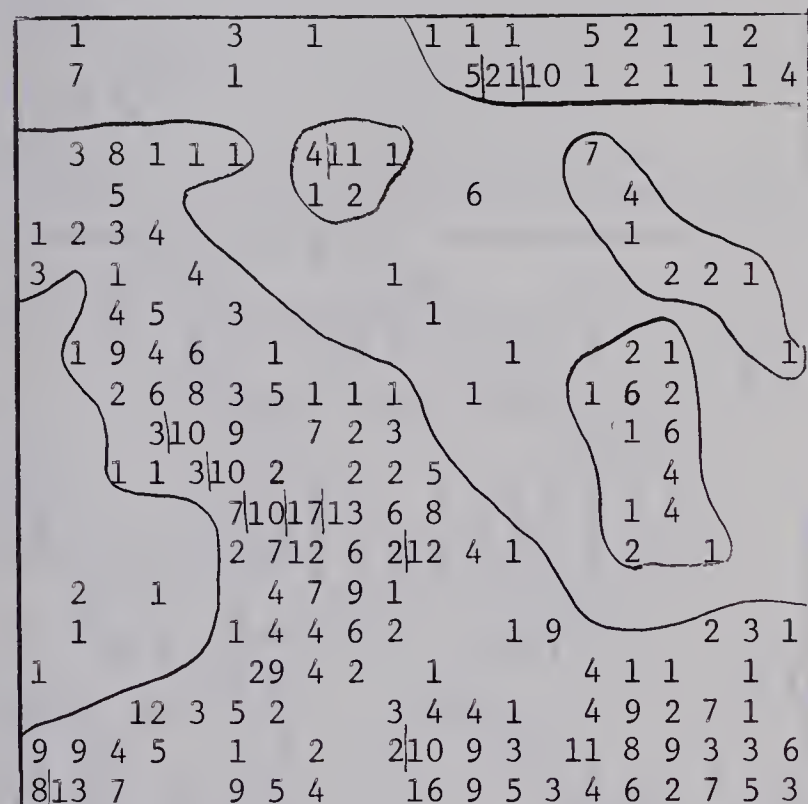


24-J-I

```

numbers = actual
numbers of individuals

```



24-J-I

The map displays the following sampling stations and their data:

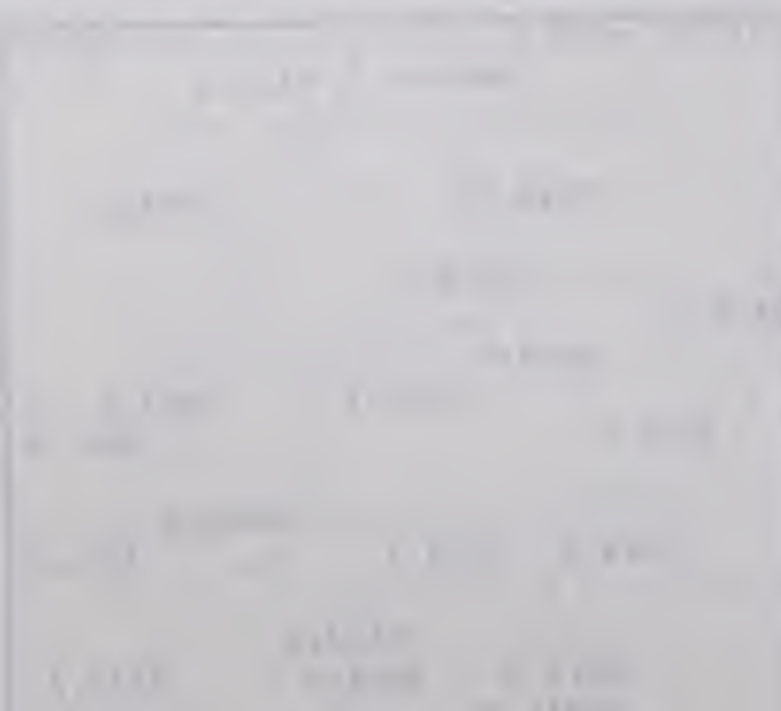
| Station Number | Salinity (S) | Temperature (T) in °C |
|----------------|--------------|-----------------------|
| 92 | 7.9 | 4.3 |
| 49 | 2.4 | 8.2 |
| 90 | 9.4 | 1.7 |
| 61 | 3.4 | 3.9 |
| 52 | 7.3 | 3.7 |
| 50 | 4.3 | 2.1 |
| 63 | 5.8 | 5.8 |
| 56 | 3.5 | 3.0 |
| 62 | 5.6 | 1.6 |
| 50 | 2.2 | 2.2 |
| 84 | 8.8 | 4.5 |
| 35 | 1.6 | 4.5 |
| 90 | 9.4 | 1.7 |
| 54 | 1.7 | 3.9 |
| 64 | 3.9 | 3.9 |
| 48 | 1.5 | 1.5 |
| 60 | 1.8 | 1.8 |
| 53 | 3.7 | 3.7 |
| 96 | 11.9 | 11.9 |
| 15 | 2.2 | 2.2 |



Topographic Map
 of the
 Mountainous Region
 of the State of
 California
 showing the
 principal features
 of the terrain
 and the
 principal
 rivers and
 streams.



Topographic Map
 of the
 River Valley
 of the State of
 California
 showing the
 principal features
 of the terrain
 and the
 principal
 rivers and
 streams.



Topographic Map
 of the
 Coastal Region
 of the State of
 California
 showing the
 principal features
 of the terrain
 and the
 principal
 rivers and
 streams.

FIGURE 199

24-J-I

Pinus contorta
transgressives

numbers = actual
numbers of individuals.

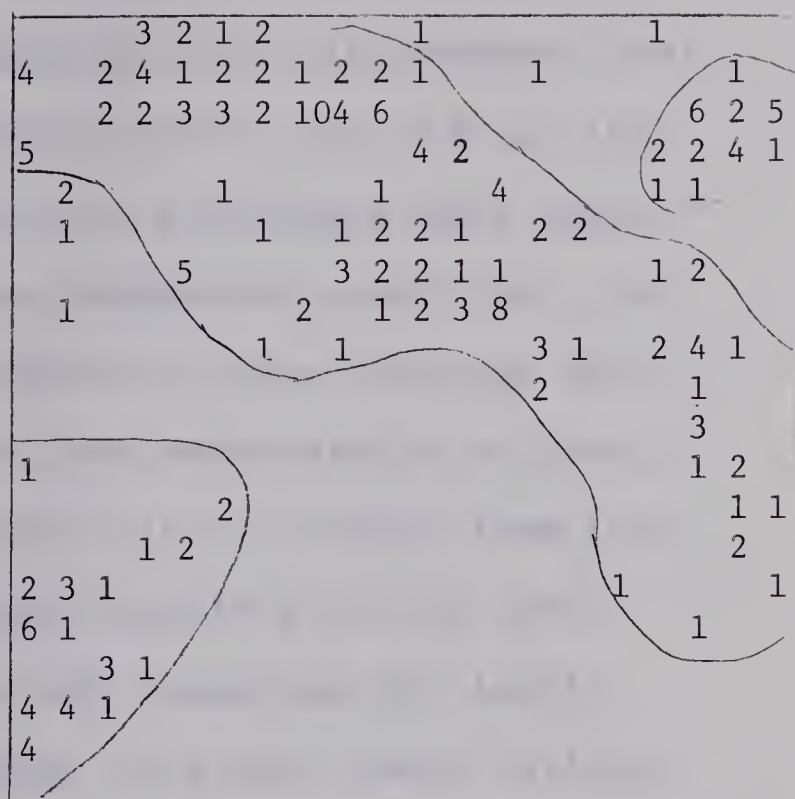


FIGURE 200

24-J-I

Pinus contorta
dead transgressives

numbers = actual
numbers of individuals.

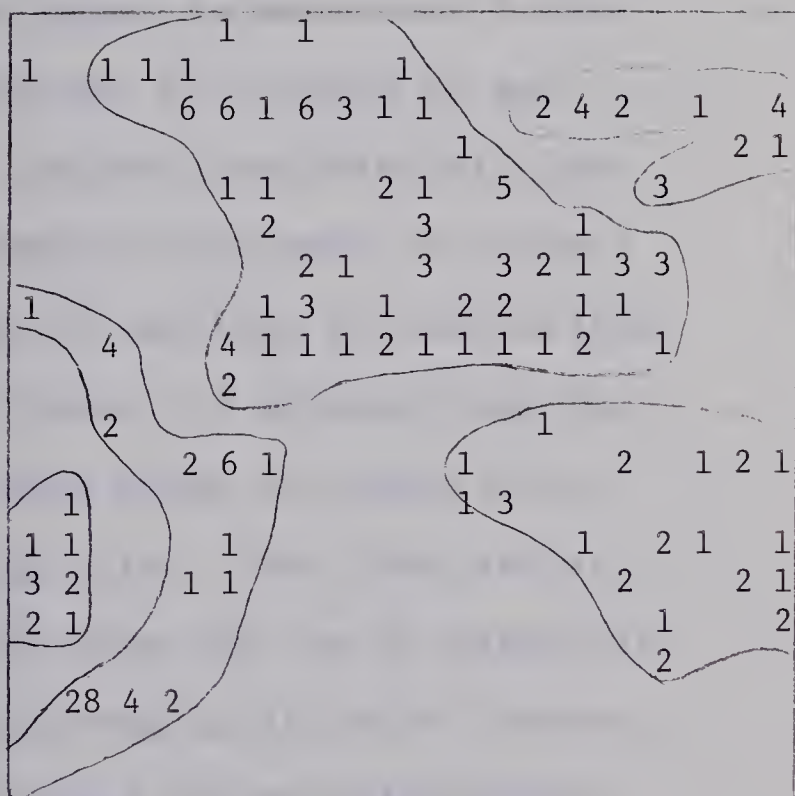


Fig.195. When compared with the tree distribution in Fig.194 and the topographic map (Fig.16) it is apparent that seedlings survive to reach transgressive size only in the open flat areas. This supports the hypothesis that pines are shade intolerant and cannot regenerate under their own canopy. But as hypothesized earlier, these openings are present presumably because they are unfavourable to tree establishment. That this is still so is evident from the high mortality of transgressives (Fig.199) in the openings even though the pines are not competing for light.

The distribution of saplings (Fig.196) lends further support to the above ideas but seems to represent a more complex situation. Individuals may be classed as saplings if they are either very reduced specimens of older age-classes or if they are advanced specimens of younger classes. Because the majority of saplings are associated with the denser areas of pine trees, it appears that the saplings represent the last major group of individuals to become established following fire. That they are so numerous (*ca.* 200 stems) and not very old (*ca.* 20 years) is indicative of slow regeneration even in the more favourable areas. Because these saplings became established after the majority of the trees, they had much greater competition as evidenced by their high mortality, especially in the densest areas of pine. That there are a few living individuals in the open areas indicates that even these areas may become forested in time. Yet, relatively

high mortality in the openings emphasizes the great difficulty experienced by trees in becoming established in these areas.

When Fig. 194 is compared with the topographic map, it can be seen that the areas of greatest tree density occur on the large dune and also in isolated clumps beyond. Whether or not these small groups of trees are associated with accumulations of fine material is not known. Fig. 194

shows that the trees in the dense areas are 30 - 40 years younger than in the openings, indicating that the dense areas have resulted from a fire which did not seriously affect the trees in the open areas.

The complete lack of deadfall from the previous forest indicates that the area was burned at least once after the fire which originally destroyed the prior forest. Such ground fires usually consume all or most of the deadwood which has fallen (MacDonald, personal communication¹).

Stand 24-J-I has little evidence to suggest succession to *Abies* or *Picea*. Table 14 shows only four *Picea mariana* and one *Picea glauca* tree in the entire hectare studied. The former are restricted to the terrace edge in the southwest and the latter appears to be a tree which became established with the majority of the pine. Although several seedlings of *Picea glauca* and *Abies lasiocarpa* were found, mortality is extremely high. At this rate of invasion, it will take a very long time before the pine are replaced. Within recent years at least, there has been the added

¹Alberta Forest Service, Dep. of Lands and Forests

factor of heavy browsing by the large herbivore populations. The *Abies* appears to be the most susceptible to browse. Trampling may also be important, but specific data are not available.

THE SUBORDINATE STRATA

The dispersion patterns of many subordinate species may be well correlated with the distribution of the pine trees and more specifically with their density patterns. The following species show a strong positive correlation with pine density:

| | | |
|---|----------------------------|----------------------------|
| * <i>Hylocomium splendens</i> (Fig.201) | <i>Pyrola virens</i> | (Fig.202) |
| * <i>Pleurozium schreberi</i> (Fig.201) | <i>Populus tremuloides</i> | (Fig.204) |
| <i>Pyrola secunda</i> | (Fig.203) | <i>Salix</i> sp. (Fig.205) |
| <i>Shepherdia canadensis</i> (Fig.207) | | |

Some of the subordinate species appear associated with a narrow transition zone between the dense and the open areas of pine: *Arctostaphylos uva-ursi* (Fig. 210), *Linnaea borealis* (Fig. 211), and *Amelanchier alnifolia* (Fig. 209). The *Linnaea* was seen to occur in more "protected" areas than those where *Arctostaphylos* occurred. The latter species was often found between the *Linnaea* and the open, drier areas of the stand.

Species reaching their greatest abundance and vigour in the more open areas of the stand are.

*The *Hylocomium* and *Pleurozium* were not noted separately in the field in this stand, but were included in the category "mosses". Mosses other than these two were relatively insignificant in abundance.

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THE JOURNAL OF THE
ROYAL ANTHROPOLOGICAL INSTITUTE

VOL. LXXV. PART 1. 1945.

FIGURE 201

'Mosses'

24-J-I

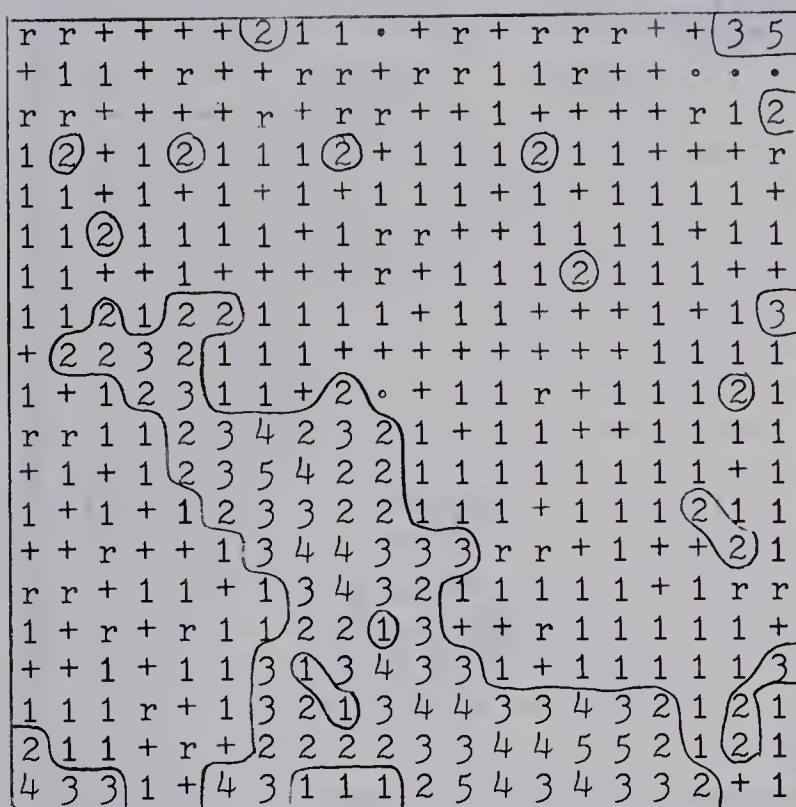


FIGURE 202

Pyrola virens

24-J-I

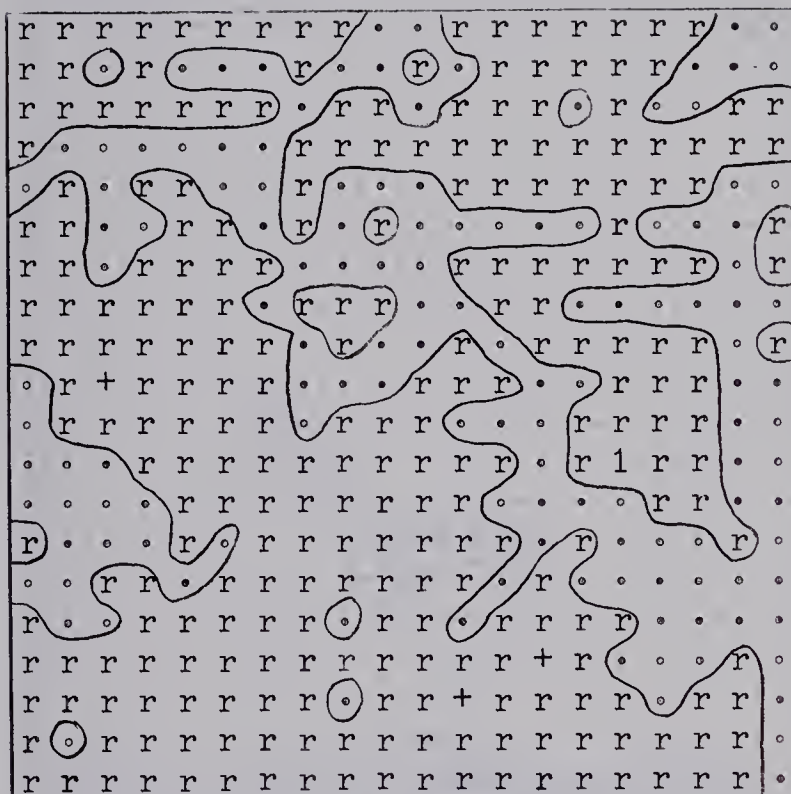


FIGURE 203

Pyrola secunda

24-J-I

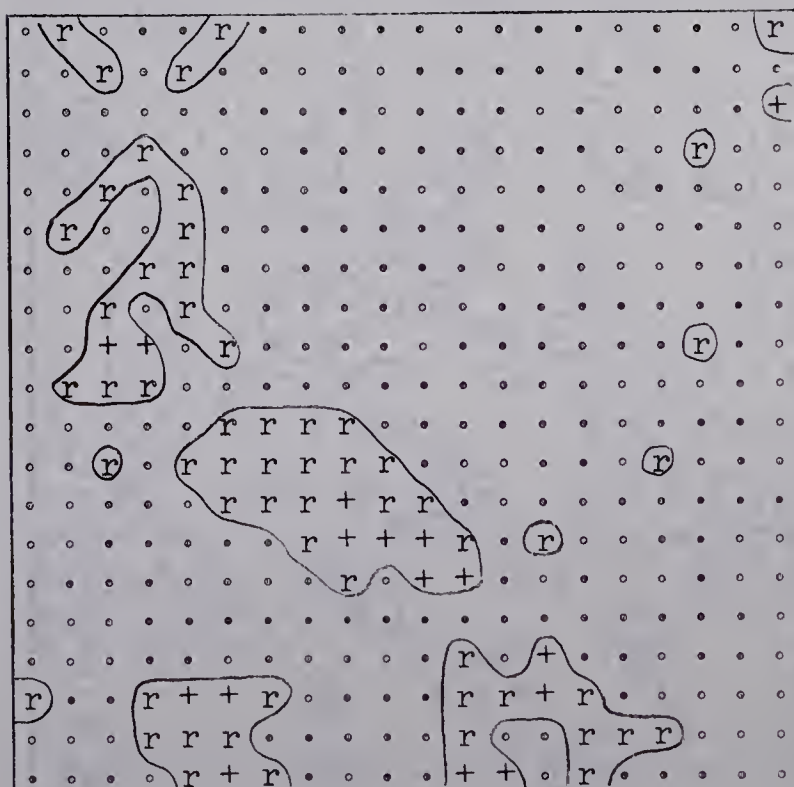


FIGURE 204

Populus tremuloides

24-J-I

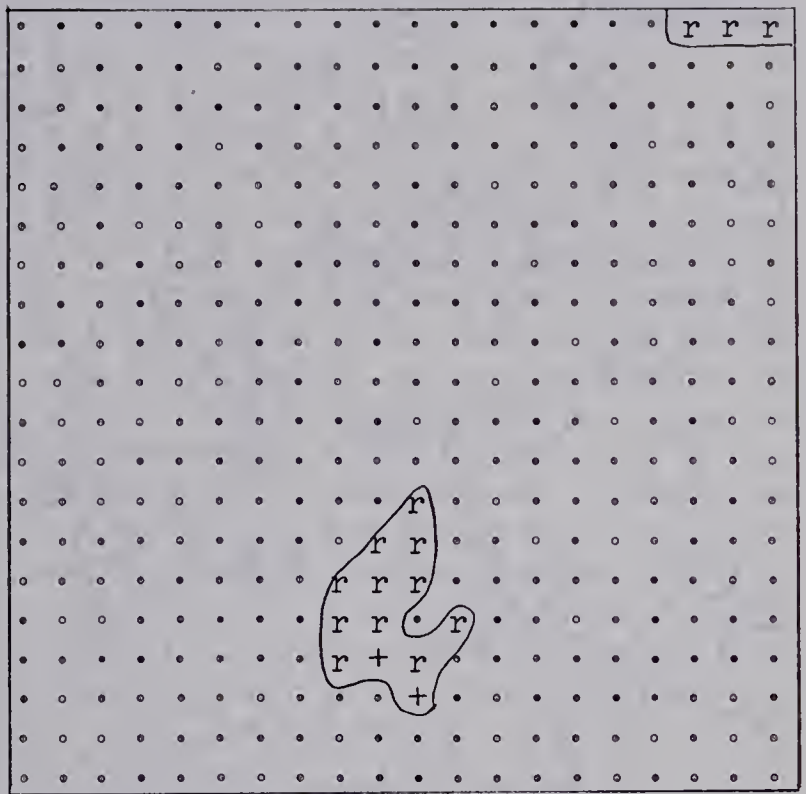


FIGURE 205

Salix spp.

24-J-I

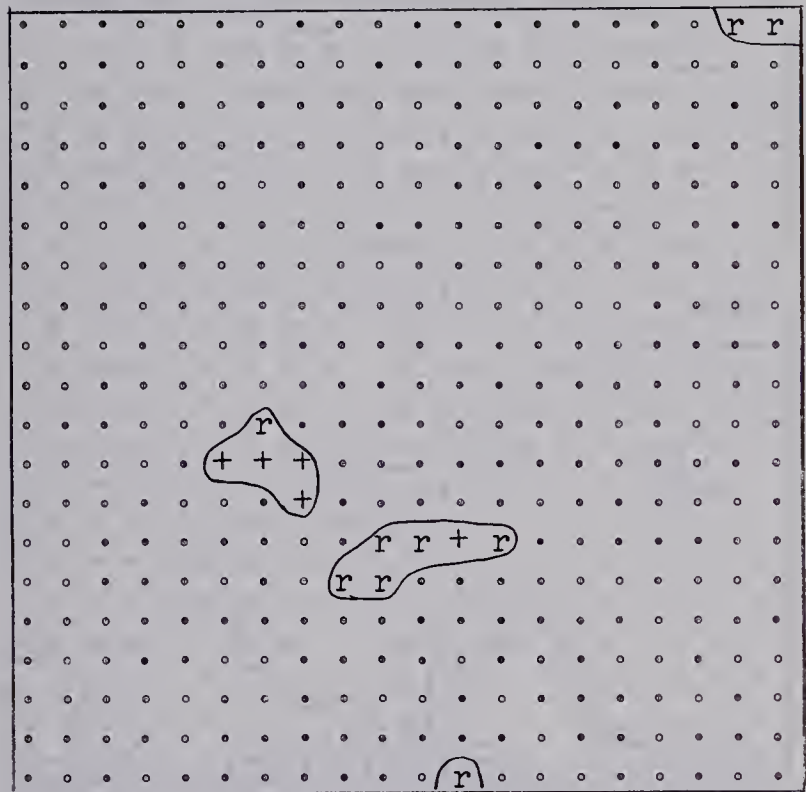
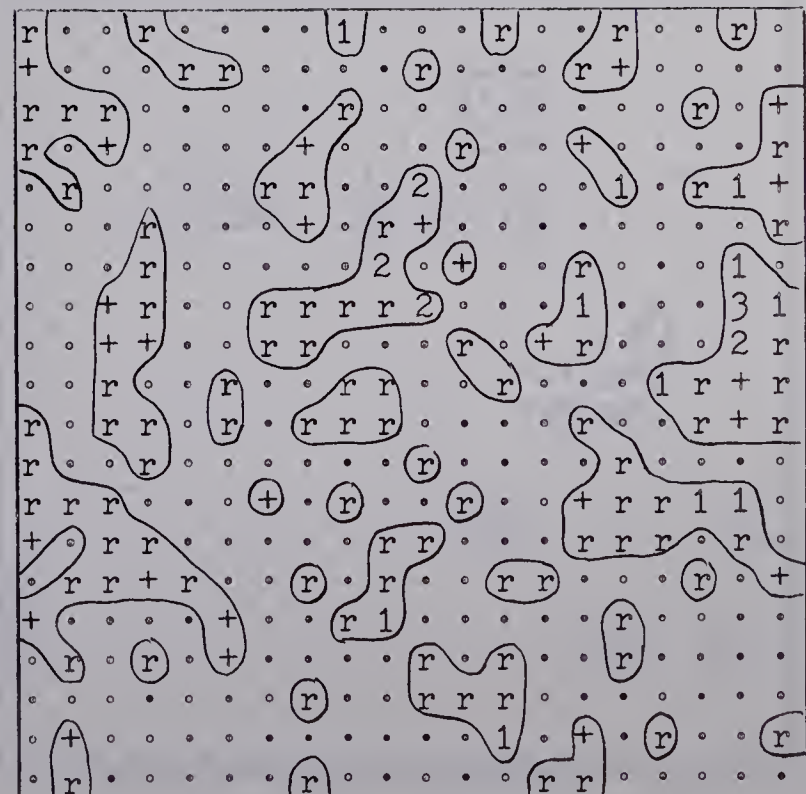


FIGURE 206

Juniperus communis

24-J-I





1000
 1000
 1000



1000
 1000
 1000



1000
 1000
 1000

FIGURE 207

Shepherdia canadensis

24-J-I

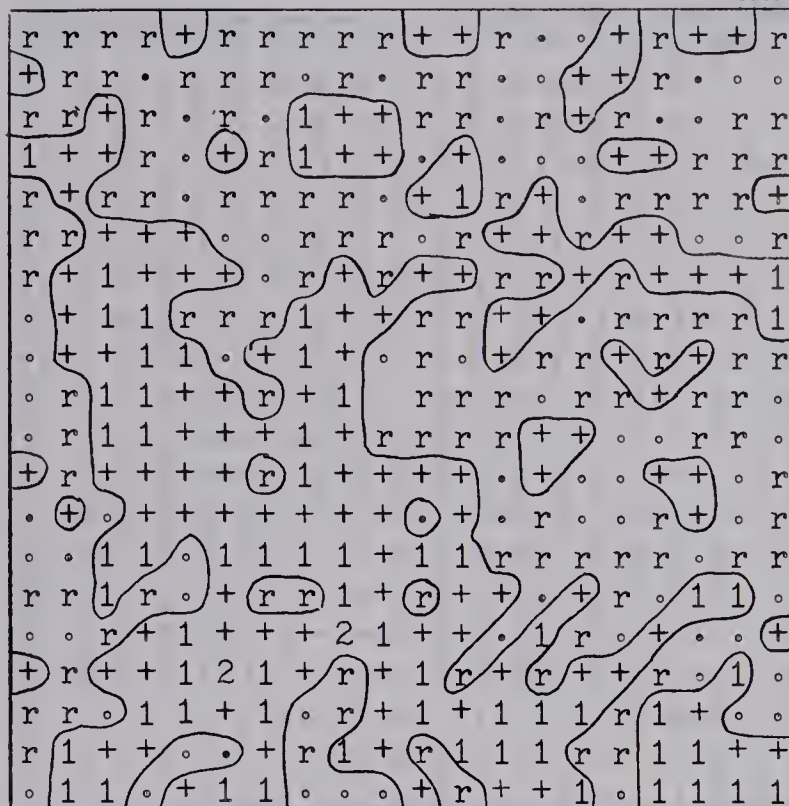


FIGURE 208

Rosa acicularis

24-J-I

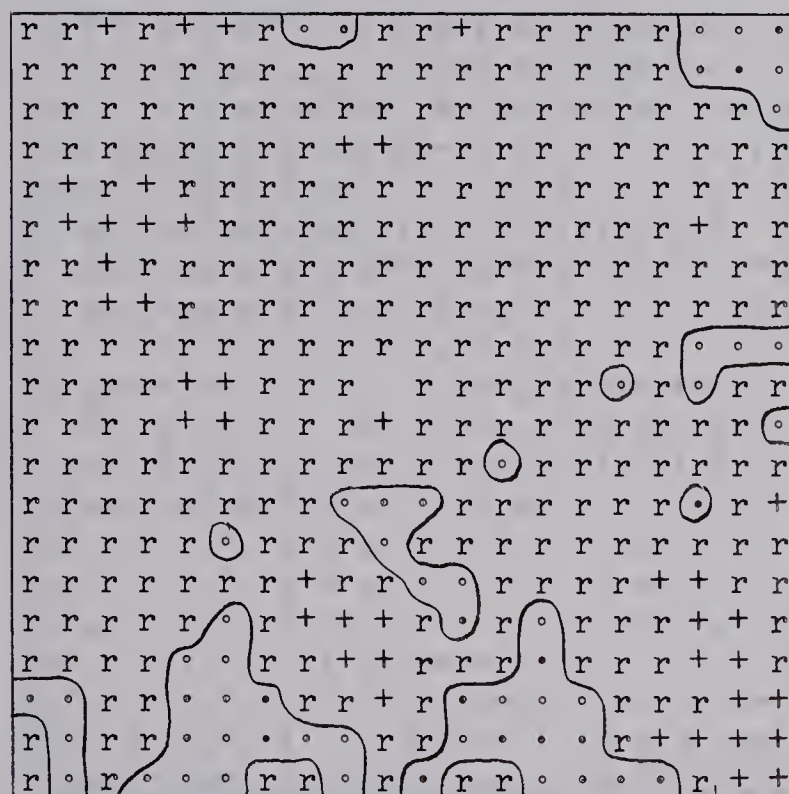
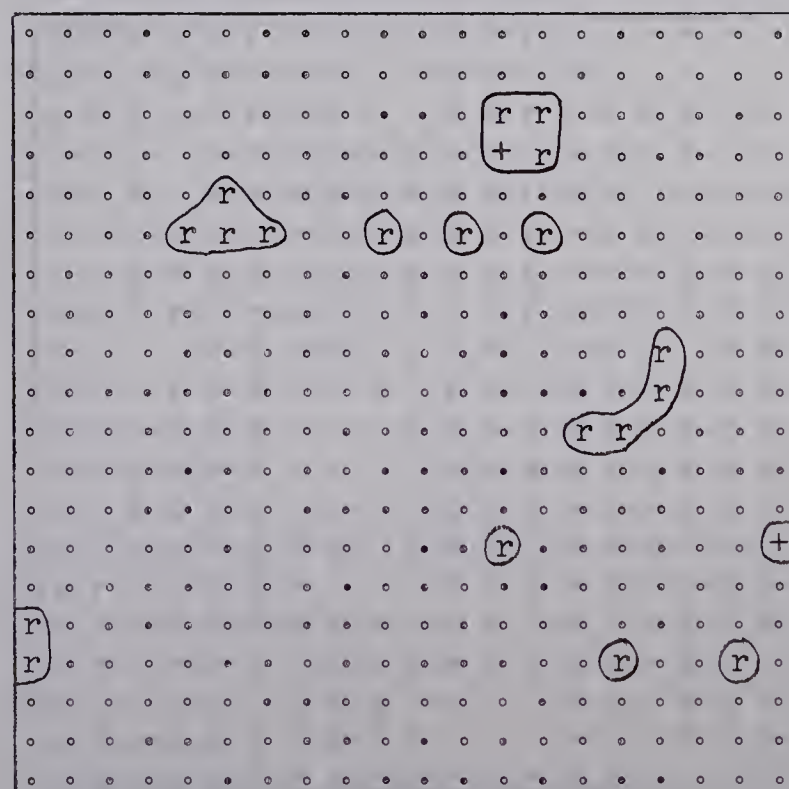


FIGURE 209

Amelanchier alnifolia

24-J-I

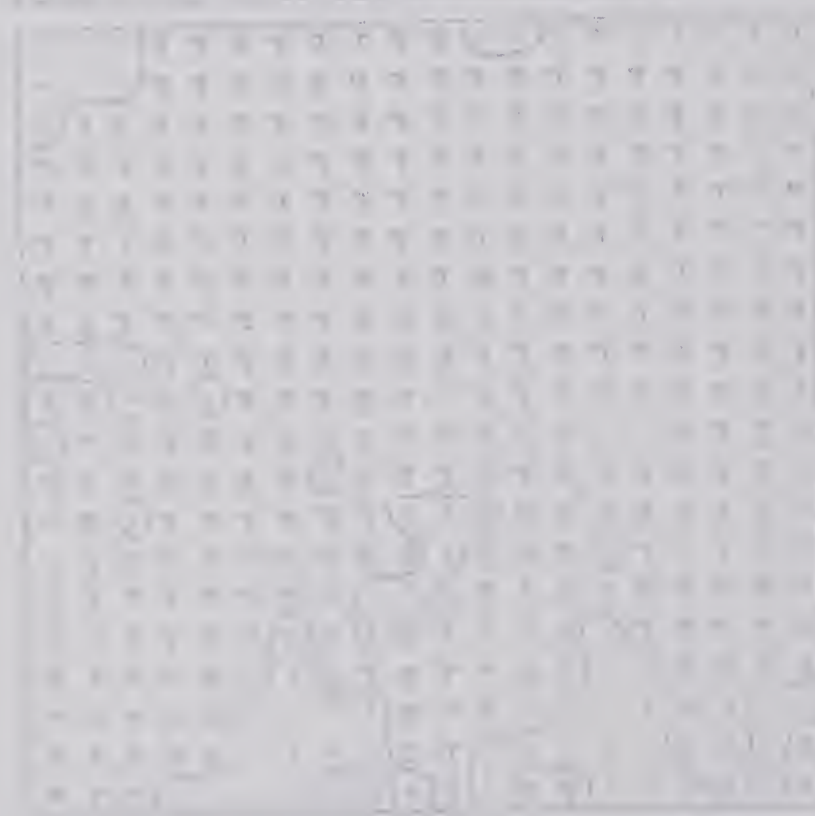




1-1-11

1-1-11

1-1-11



1-1-11

1-1-11

1-1-11



1-1-11

1-1-11

1-1-11

FIGURE 210

Arctostaphylos uva-ursi

24-J-I

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4 | 2 | 2 | + | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 4 | 2 | 4 | 4 | 1 | 1 | 2 | + | r |
| 1 | 2 | 2 | 3 | 2 | 1 | 2 | 4 | 4 | 3 | 3 | 2 | 1 | 2 | 2 | 1 | 2 | . | . | . |
| 2 | 2 | 1 | 1 | 2 | 1 | 2 | 4 | 3 | 1 | 1 | 1 | + | + | 2 | 2 | + | + | r | + |
| 1 | 1 | 2 | 1 | 3 | 2 | 1 | 3 | 1 | 3 | 3 | 2 | 3 | 3 | 2 | 2 | 3 | 2 | + | 1 |
| 2 | 1 | r | 2 | 2 | 1 | 2 | + | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | r | 1 | 3 |
| 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 3 | 3 | 2 | 1 |
| 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | + | 1 | 2 |
| 2 | 2 | + | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 3 | 3 | 2 | 3 | 2 | 2 | 1 |
| 2 | 1 | 1 | + | 1 | 2 | + | 3 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 3 | 1 | 1 | 1 | 1 |
| 1 | 1 | 1 | 1 | 2 | 2 | 3 | 3 | 3 | | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | + | + |
| 2 | 3 | 3 | 2 | + | + | r | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 1 |
| 2 | 3 | 3 | 2 | + | + | r | r | + | 1 | 1 | + | 1 | 1 | 1 | 1 | + | 2 | 3 | 2 |
| 1 | 2 | 2 | 3 | 2 | 1 | 1 | 1 | 2 | + | 1 | 2 | + | 2 | 1 | 2 | 1 | + | 2 | 2 |
| 1 | 3 | 2 | 2 | 2 | 2 | 1 | r | 1 | + | + | 2 | 2 | 1 | 2 | 2 | 2 | 3 | 3 | 1 |
| 4 | 2 | 1 | 1 | 3 | 4 | + | + | r | 1 | 2 | 2 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 1 |
| 2 | 3 | 3 | 3 | 2 | 2 | 1 | + | + | r | 1 | 3 | 2 | 3 | 3 | + | 2 | 1 | 1 | 2 |
| 2 | 2 | 2 | 3 | 1 | 3 | r | 1 | 1 | r | + | + | 2 | + | 2 | 1 | 2 | 1 | 2 | r |
| 2 | 2 | 1 | 3 | + | 1 | 1 | 1 | + | + | 1 | 1 | 1 | + | 2 | 3 | 4 | 4 | 3 | 3 |
| 2 | 4 | 5 | 4 | 4 | 4 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | + | + | 1 | 2 | 1 | 1 |
| + | 2 | 1 | 3 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | + | 1 | 1 | 1 | 2 | 2 |

FIGURE 211

Linnaea borealis

24-J-I

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 1 | + | r | + | r | 2 | + | r | r | r | 1 | + | . | r | . | + | + | 1 | + |
| + | 1 | 1 | + | 1 | r | . | . | . | . | 1 | 2 | + | + | 1 | + | r | . | . | . |
| + | 1 | 1 | + | + | r | r | + | r | . | + | . | r | r | + | r | . | r | + | + |
| + | 1 | 1 | 1 | 1 | 1 | r | + | + | r | + | 1 | 1 | 1 | + | + | r | . | r | r |
| + | + | 1 | 1 | + | 1 | 1 | + | 1 | . | . | 1 | 1 | 1 | 1 | . | . | r | . | + |
| 1 | r | + | + | + | + | r | r | . | r | . | . | 1 | 1 | 1 | 1 | + | + | . | . |
| . | 1 | . | + | r | r | 1 | + | r | + | r | r | + | r | r | r | + | 1 | + | 1 |
| . | r | + | + | + | r | + | + | + | + | + | + | + | . | . | . | . | . | r | r |
| . | . | + | + | . | . | . | 1 | r | . | r | + | 1 | 1 | 1 | . | . | . | + | . |
| r | 1 | + | + | r | . | . | . | . | . | . | + | 1 | r | + | + | + | r | . | . |
| . | + | 1 | 1 | + | . | . | . | r | . | . | + | . | + | + | r | + | 1 | r | . |
| . | + | + | 1 | 1 | r | r | r | + | + | r | + | r | . | 1 | . | 1 | 1 | . | . |
| r | + | + | r | r | + | 2 | + | + | r | . | + | r | . | . | . | . | . | . | . |
| . | . | + | . | . | . | 1 | + | r | . | . | . | + | . | . | + | . | . | . | . |
| r | . | . | . | . | . | + | 1 | + | r | . | . | . | . | . | . | r | . | + | . |
| + | r | . | . | 1 | . | + | + | r | r | . | . | . | . | . | + | . | r | . | + |
| + | . | . | . | . | r | . | 1 | 1 | r | + | + | + | . | . | . | . | . | . | r |
| . | . | . | . | 1 | r | . | + | . | r | r | r | r | . | . | . | . | + | r | . |
| r | 1 | + | r | r | . | 1 | . | . | r | r | + | . | . | . | r | r | r | r | + |
| + | + | 1 | 1 | + | . | 1 | + | . | 1 | + | r | . | . | . | r | 1 | + | + | + |

FIGURE 212

Achillea millefolium

24-J-I

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| r | r | r | r | r | r | r | r | r | r | r | r | + | r | r | r | r | r | r | r | ° |
| r | + | ° | r | r | r | r | r | r | r | r | r | r | ° | ° | ° | ° | r | ° | ° | ° |
| r | r | r | r | ° | r | r | r | r | ° | r | r | r | r | r | r | r | r | r | r | ° |
| r | r | r | ° | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r |
| r | r | r | ° | r | r | r | r | r | r | r | r | r | r | r | r | ° | r | r | r | r |
| ° | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r |
| ° | ° | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r |
| r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | r | + | r | r |
| + | r | ° | ° | r | r | r | r | r | r | r | r | r | r | r | r | r | ° | r | r | r |
| r | r | ° | r | r | r | r | r | r | | r | r | r | r | r | r | r | r | r | r | ° |
| r | r | r | r | r | r | r | ° | r | r | r | r | r | r | r | r | r | r | r | r | r |
| r | r | r | r | r | ° | r | ° | ° | ° | r | r | r | r | r | r | r | r | r | r | ° |
| r | r | r | r | r | r | ° | r | r | ° | r | r | r | r | r | r | r | r | r | r | r |
| r | r | r | r | r | r | r | r | ° | r | r | r | r | r | r | r | r | r | r | r | r |
| r | r | r | r | r | r | r | ° | ° | ° | r | r | r | r | r | r | r | r | r | r | r |
| r | r | r | r | r | r | r | r | ° | r | r | r | r | ° | r | r | r | r | r | r | r |
| r | r | r | r | r | r | ° | 1 | r | r | r | r | r | r | r | r | r | r | r | r | r |
| r | r | r | r | r | ° | r | r | r | ° | r | ° | ° | r | r | r | r | r | r | r | r |
| r | r | r | r | r | r | r | r | r | r | ° | r | ° | r | ° | r | r | ° | r | ° | ° |
| ° | r | r | r | r | r | r | r | r | r | ° | r | ° | r | r | ° | ° | r | ° | ° | ° |

Antennaria nitida (Fig. 214) *Festuca saximontana* (Fig. 216)
Calamagrostis purpurescens (Fig. 215) *Juniperus communis* (Fig. 206)
Senecio cymbalarioides (Fig. 218)

Species such as *Fragaria virginiana* (Fig. 223), *Achillea millefolium* (Fig. 212), and *Rosa acicularis* (Fig. 208) appear regularly dispersed, being absent only from the dense thickets of pine and from the extremely xeric site in the southwest corner of the plot.

From field observations it would appear that factors such as shading, and aspect due to microtopography, which modify the intensity of solar radiation received per unit ground area, are important factors controlling the distribution of the subordinate species. In this particular stand, trampling caused by large herbivores is also partly responsible for the impoverishment of the vegetation in certain areas.

XI. SOIL

The data gathered concerning the within-stand variation in available soil nutrients and the seasonal fluctuation of these nutrients are not sufficiently detailed to permit correlations to be made with the observed species distribution patterns within the five Intensive Stands. Analyses for available nutrients, pH etc. of surface soil samples (0-15 cm) collected in 1967 in the 25 intensively studied quadrats of stand 47-B-I, indicated the uneven distribution of quantities of these edaphic factors (see Table 15). The same variability was evident in the samples collected from each of the

FIGURE 213

Antennaria rosea

24-J-I

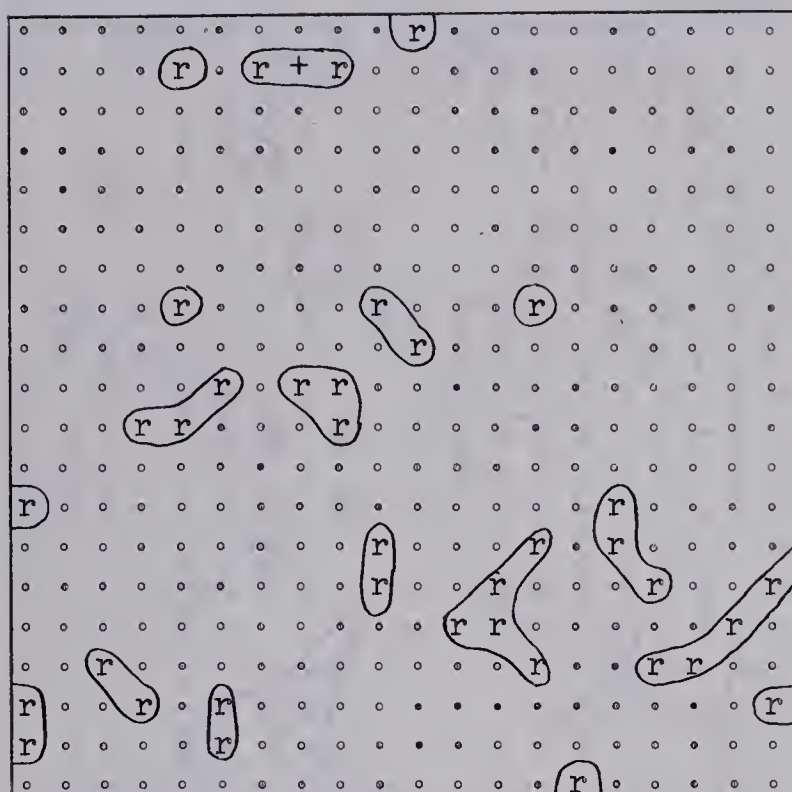


FIGURE 214

Antennaria nitida

24-J-I

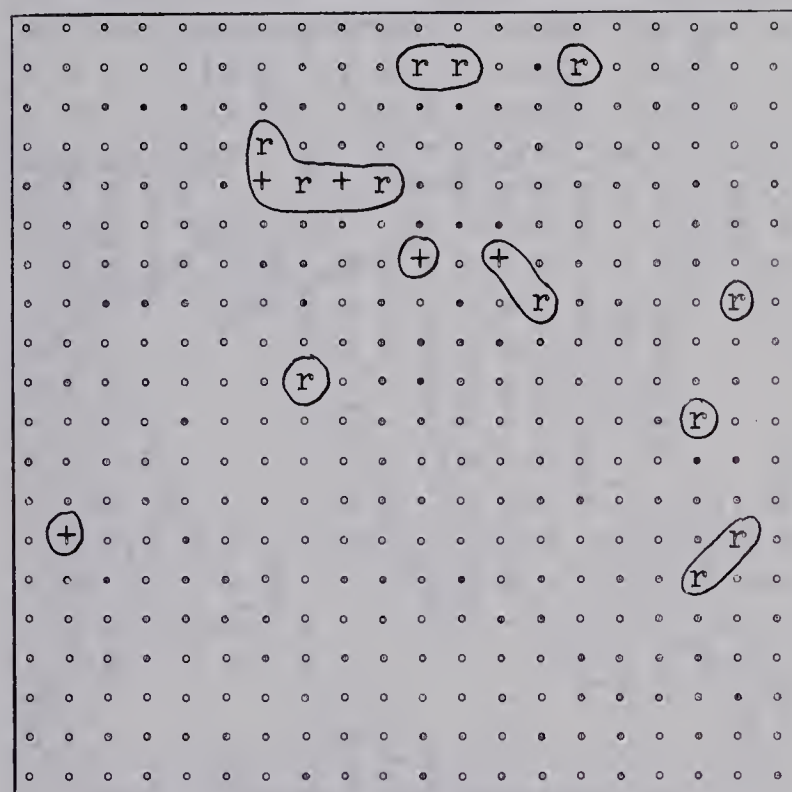


FIGURE 215

Calamagrostis purpurescens

24-J-I

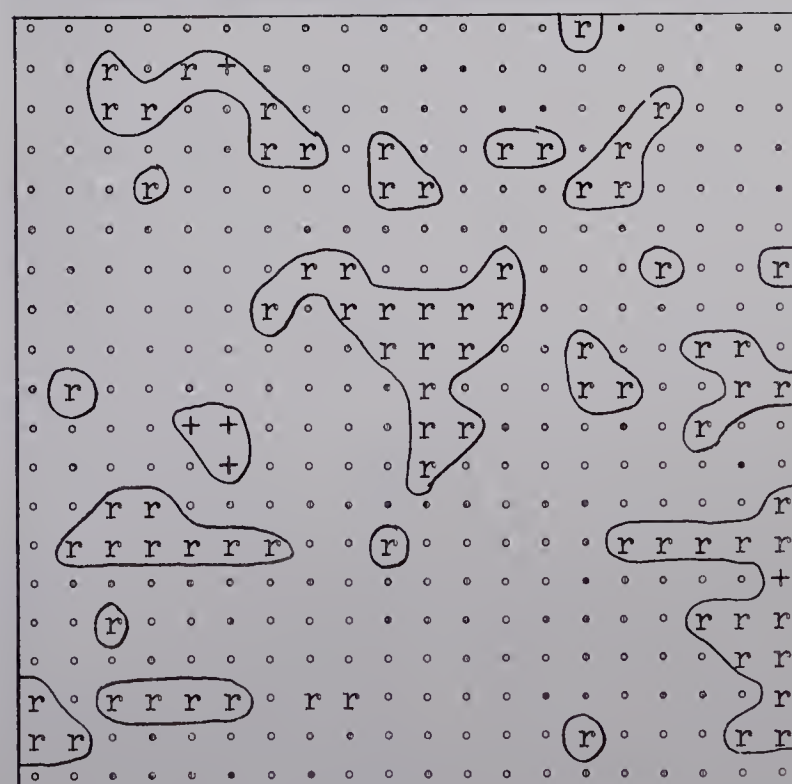


FIGURE 216

Festuca saximontana

24-J-I

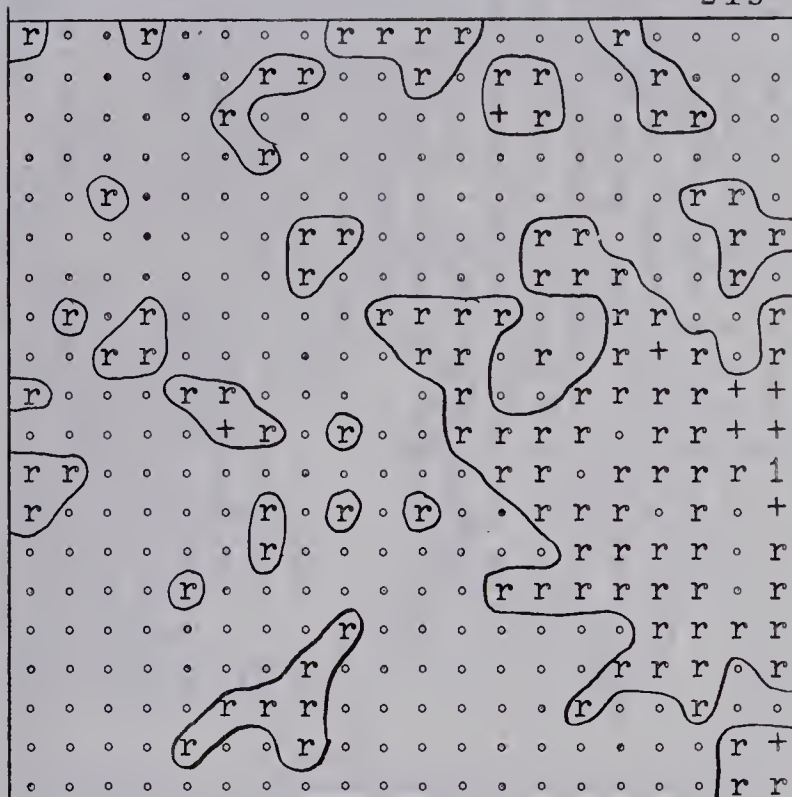


FIGURE 217

Viola adunca

24-J-I

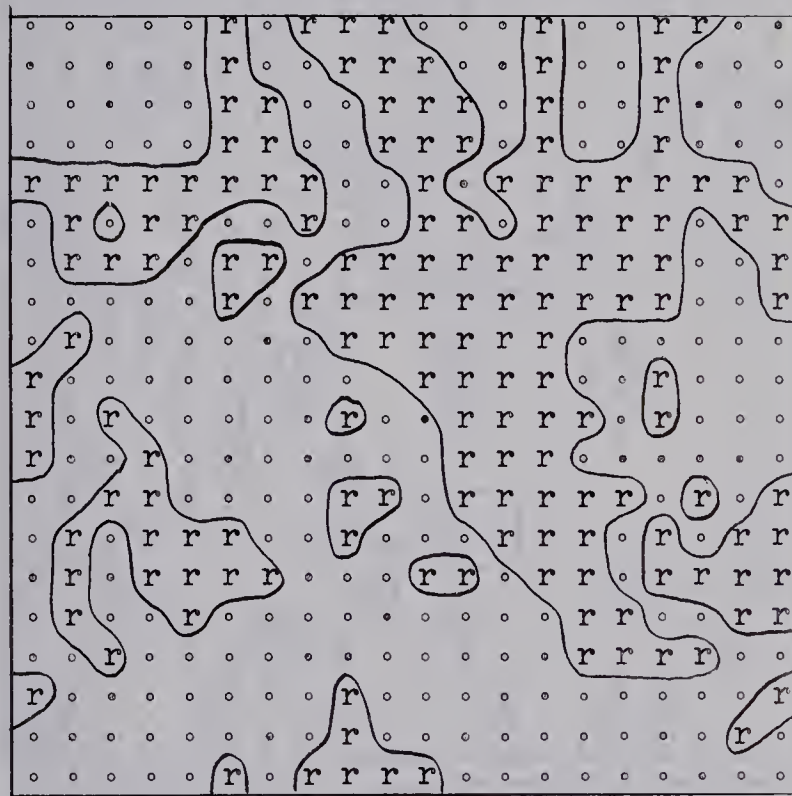


FIGURE 218

Senecio cymbalarioides

24-J-I

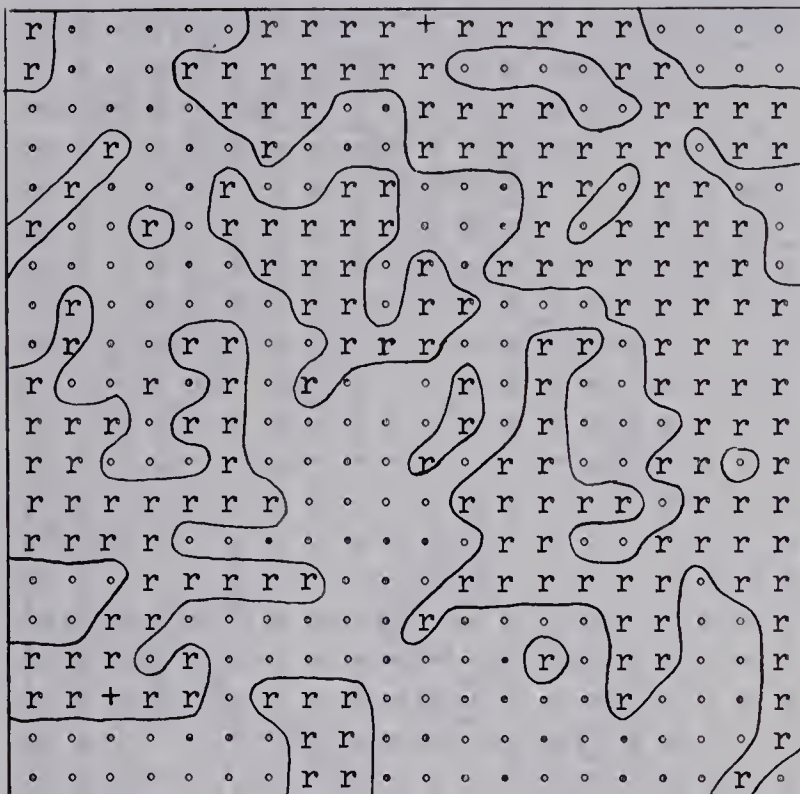


FIGURE 219

Gentianella amarella

24-J-I

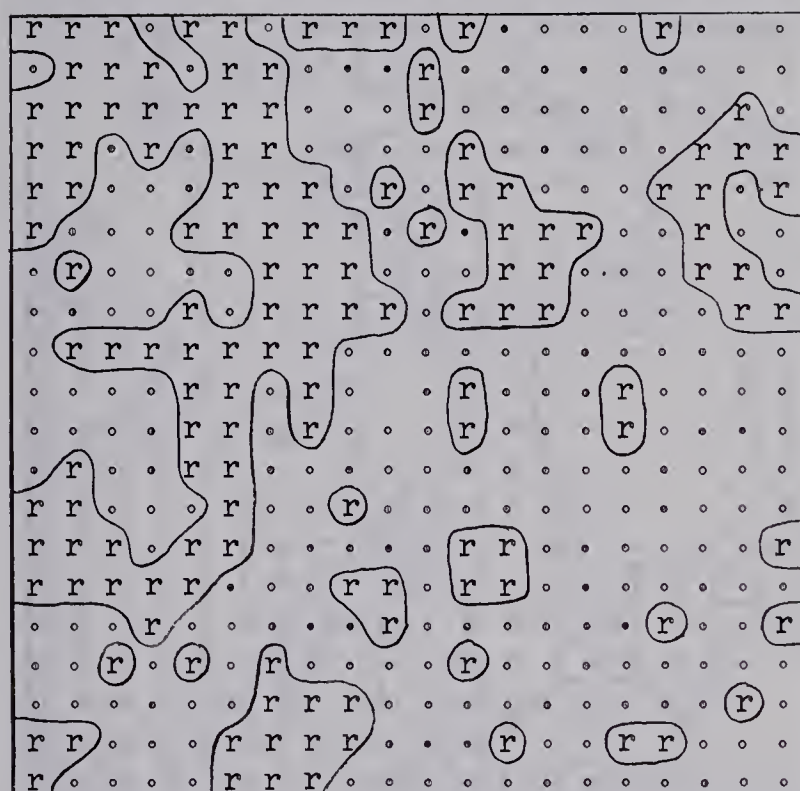


FIGURE 220

Solidago decumbens

24-J-I

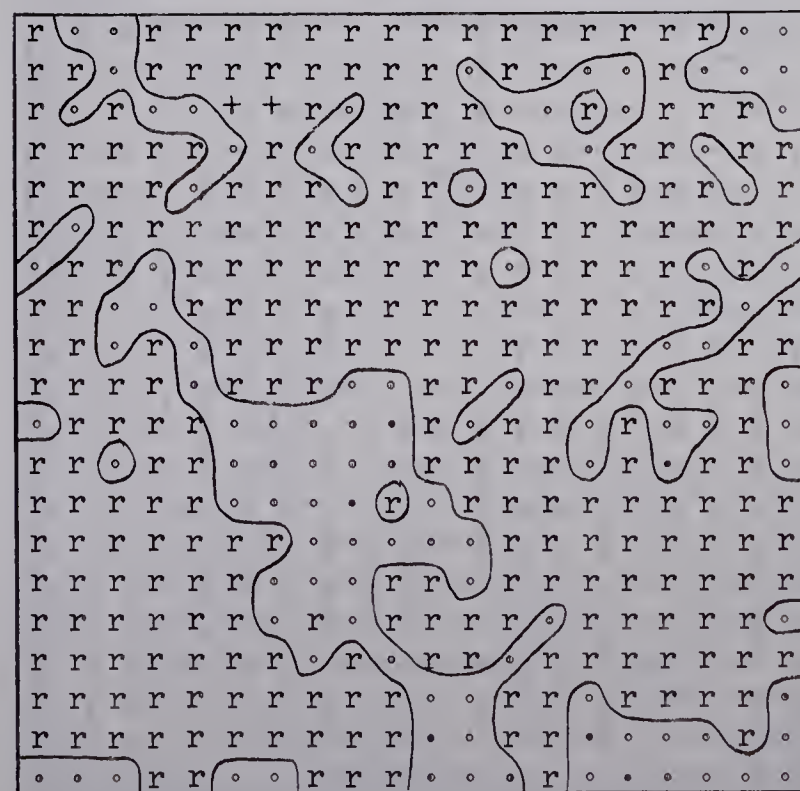


FIGURE 221

Elymus innovatus

24-J-I

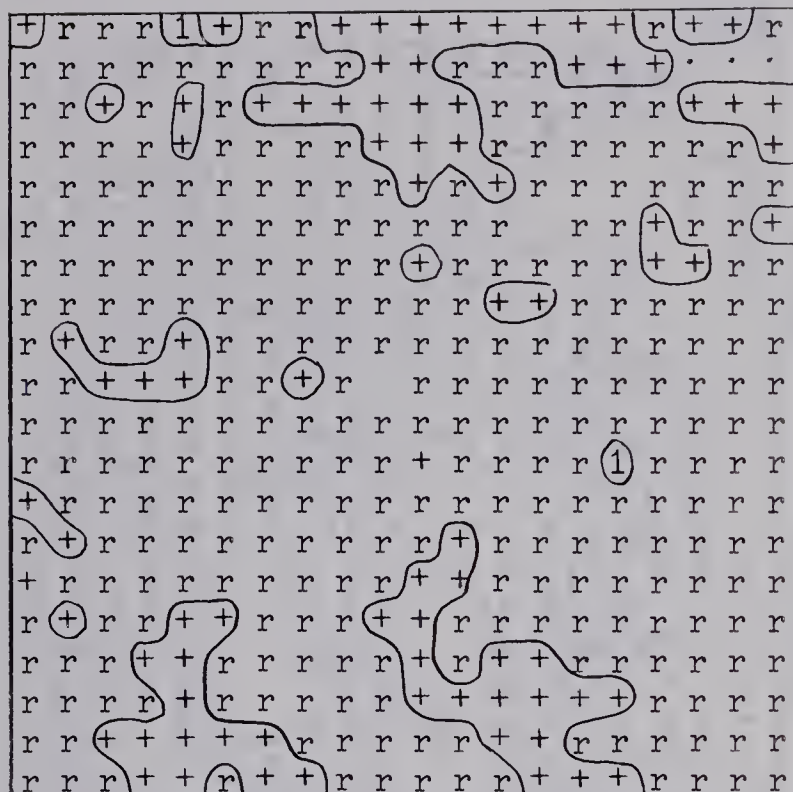


FIGURE 222

*Carex concinnoides**Carex richardsonii*

24-J-I

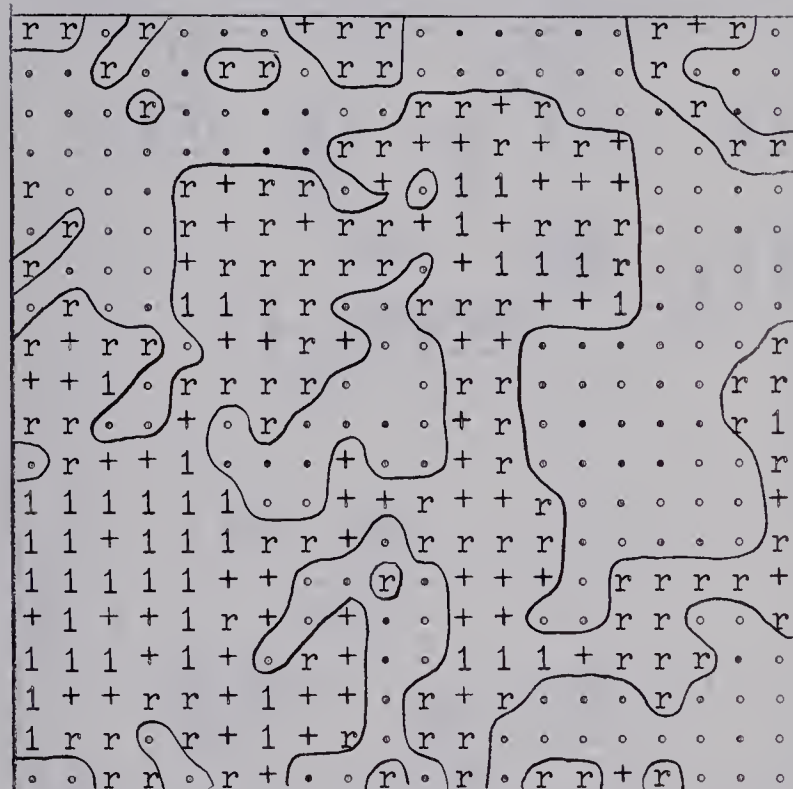


FIGURE 223

Fragaria virginiana

24-J-I

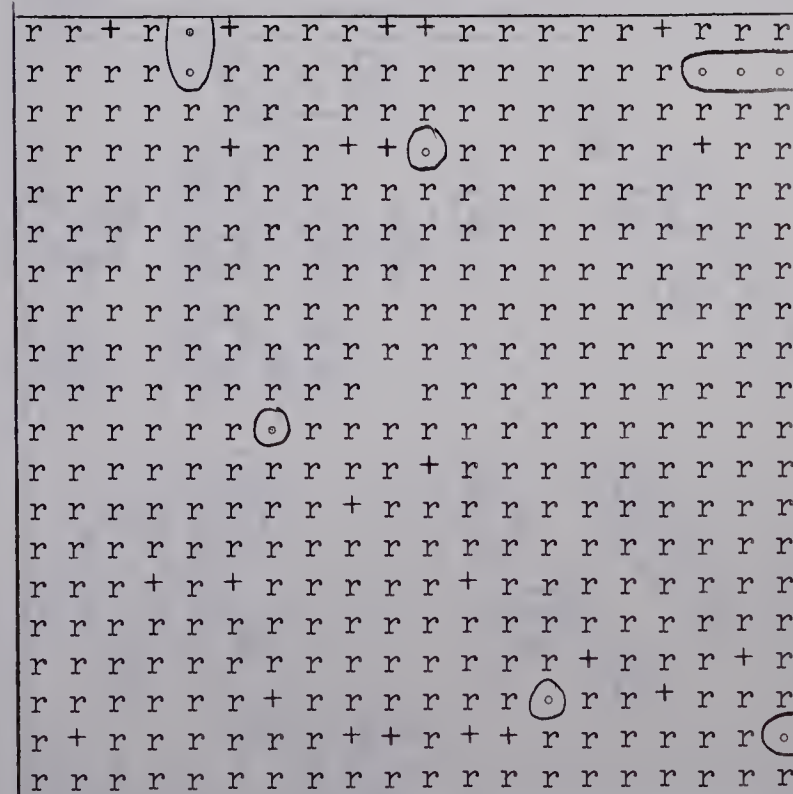


FIGURE 224

Antennaria neglecta

24-J-I

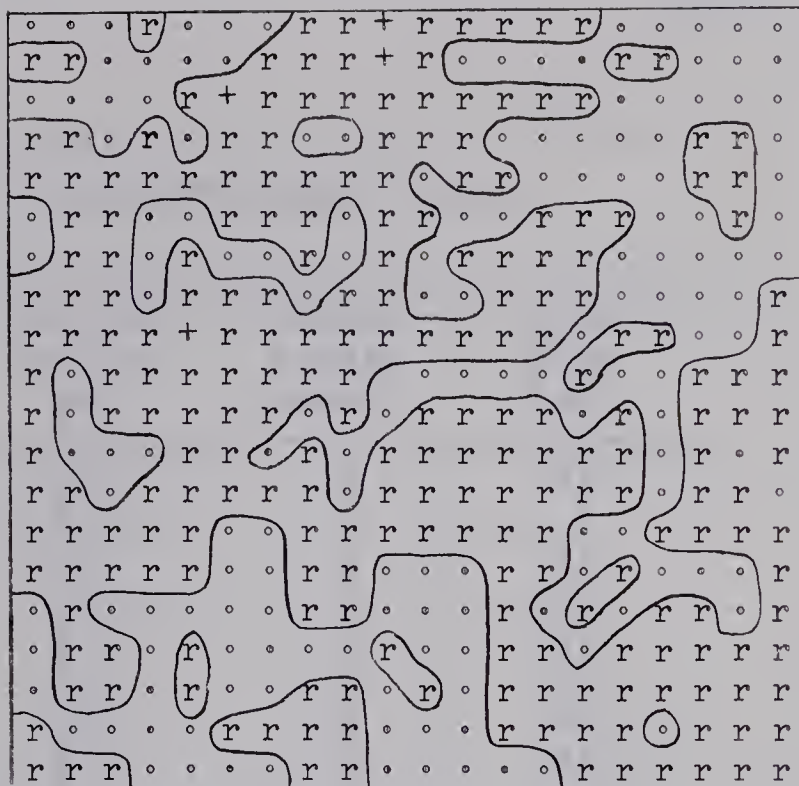


FIGURE 225

Calypso bulbosa

24-J-I

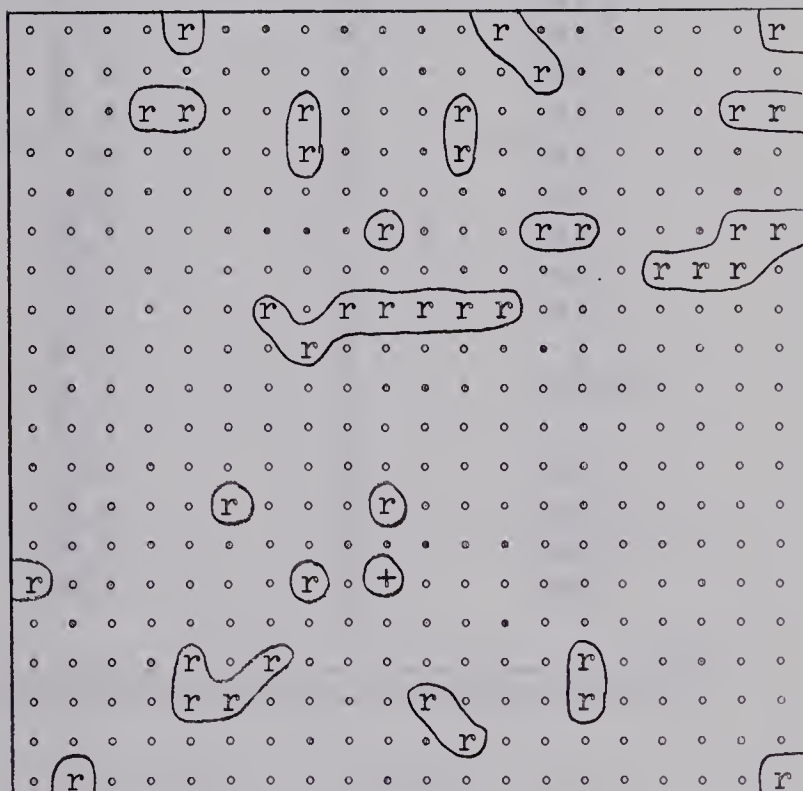


FIGURE 226

Campanula rotundifolia

24-J-I

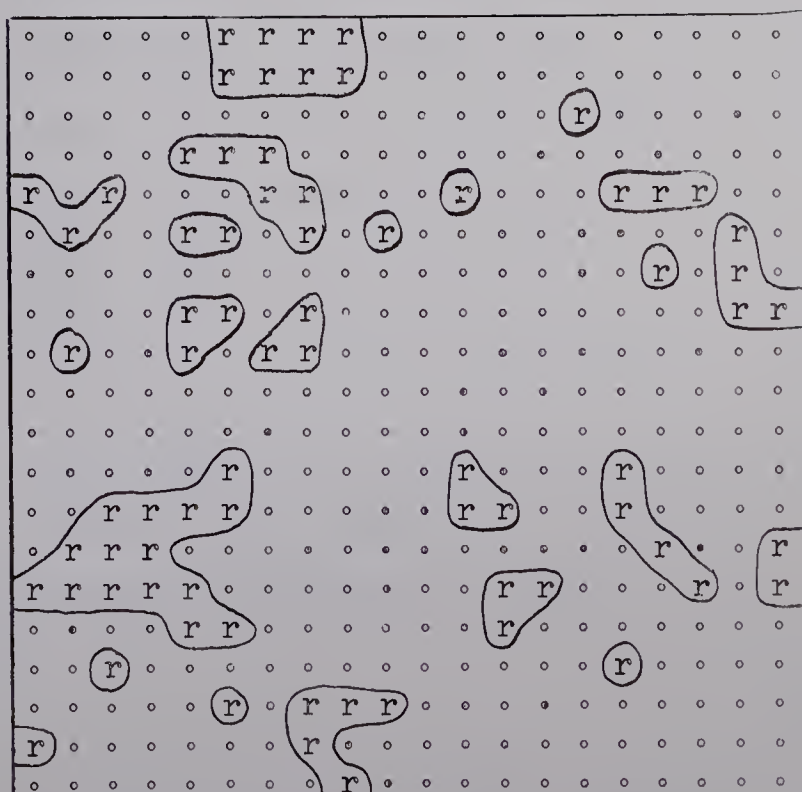


TABLE 15. EDAPHIC FACTORS OF INTENSIVE STAND 47-B-I

| Plot No. | Pounds N | per P | acre K | Soil re-action (pH) | Conduc-tivity mmhos. | Free Lime CaCO ₃ |
|----------|----------|-------|--------|---------------------|----------------------|-----------------------------|
| 47-I-A | 0 | 2 | 90 | 5.5 | .2 | nil |
| 47-I-C | 0 | 2 | 74 | 6.2 | .5 | 3 |
| 47-I-D | 0 | 7 | 59 | 5.6 | .3 | nil |
| 47-I-E | 0 | 7 | 82 | 5.8 | .2 | nil |
| 47-I-F | 0 | 2 | 90 | 5.4 | .1 | nil |
| 47-I-G | 2 | 1 | 55 | 5.5 | .1 | nil |
| 47-I-H | 0 | 2 | 110 | 5.5 | .1 | nil |
| 47-I-H | 0 | 12 | 98 | 5.0 | .1 | nil |
| 47-I-J | 0 | 1 | 55 | 5.3 | .07 | nil |
| 47-I-K | 0 | Tr | 66 | 5.4 | .07 | nil |
| 47-I-L | 0 | 2 | 62 | 5.4 | .1 | nil |
| 47-I-M | 0 | 10 | 86 | 5.4 | .1 | nil |
| 47-I-N | 0 | 4 | 94 | 5.6 | .2 | nil |
| 47-I-O | 0 | 2 | 59 | 5.3 | .1 | nil |
| 47-I-P | 0 | 7 | 82 | 4.8 | .1 | nil |
| 47-I-Q | 0 | 7 | 168 | 5.3 | .1 | nil |
| 47-I-R | 0 | 2 | 78 | 5.2 | .1 | nil |
| 47-I-T | 0 | 0 | 52 | 6.0 | .4 | 1 |
| 47-I-U | 2 | 2 | 98 | 5.7 | .1 | nil |
| 47-I-V | 1 | 2 | 55 | 5.8 | .2 | 1 |
| 47-I-W | 1 | 5 | 82 | 5.0 | .1 | nil |
| 47-I-X | 2 | 5 | 114 | 5.0 | .07 | nil |
| 47-I-Y | 3 | 10 | 102 | 4.9 | .1 | nil |
| 47-I-S | 1 | 2 | 78 | 4.8 | .07 | nil |

intensive stands studied in 1968 (see Table 16). Neither the scale of this patterning nor its relationship to the presence, absence, or abundance of the plants were determined.

The parent materials of the soils of the five intensive stands are of three major kinds: (1) colluvium (stand 41-B-I) consisting of Precambrian conglomerates, sandstones, and shales; (2) alluvium (stands 24-J-I and 26-J-I) consisting of Pre- and Lower Cambrian quartzites and sandstones plus Lower Paleozoic carbonates in 24-J-I; and (3) glaci-fluvial (?) deposits stand 55-J-I consisting of Precambrian and Lower Cambrian sandstones and quartzites with some Paleozoic dolomites, and stand 47-B-I consisting of Upper Paleozoic limestones and dolomites, Lower Cambrian quartzites, and Triassic siltstones (parent material identifications by Dr. H.A.K. Charlesworth, Department of Geology, University of Alberta).

Since the parent material of the soils in all five intensive stands is transported material composed of a mixture of rock types, it is reasonable to expect an uneven distribution of nutrients which are released from the weathering rocks. The uneven distribution of nutrients as measured at the present time will also be influenced by the contagious nature of species distribution patterns. The different species have varying degrees of effect upon their edaphic environment by causing nutrients in the soil to be redistributed by means

TABLE 16. VARIATION IN EDAPHIC FACTORS THROUGH GROWING SEASON (Intensive Stands, 1968)

| | N | | P | | K | | pH | | Cond. | | Free Lime |
|--------|-----------|-----|-----------|-----|-----------|------|-----------|-----|-----------|-----|-----------|
| | \bar{x} | Sx | \bar{x} | Sx | \bar{x} | Sx | \bar{x} | Sx | \bar{x} | Sx | \bar{x} |
| 47-I | | | | | | | | | | | |
| Spring | | | | | | | | | | | |
| 0-6 * | 0 | 0 | 7.3 | 4.8 | 71.2 | 16.4 | 5.8 | 0.7 | 0.3 | 1.0 | L |
| 6-12 | 0 | 0 | 5.6 | 2.7 | 61.0 | 12.0 | 6.9 | 0.4 | 0.5 | 0.1 | M |
| Summer | | | | | | | | | | | |
| 0-6 | 0 | 0 | 1.2 | 0.8 | 72.0 | 14.4 | 5.0 | 0.2 | 0.2 | 0.1 | nil |
| 6-12 | 0 | 0 | 1.6 | 0.6 | 60.8 | 7.4 | 6.9 | 0.4 | 0.3 | 0.0 | med. |
| Fall | | | | | | | | | | | |
| 0-6 | 0.2 | 0.5 | 2.4 | 1.5 | 72.4 | 8.8 | 5.5 | 0.2 | 0.2 | 0.1 | L+;H- |
| 6-12 | 0.6 | 0.6 | 5.2 | 2.8 | 67.8 | 12.7 | 7.2 | 0.2 | 0.3 | 0.0 | L-;M |
| 41-I | | | | | | | | | | | |
| Spring | | | | | | | | | | | |
| 0-6 | 0 | 0 | 7.4 | 2.7 | 68.0 | 14.8 | 5.5 | 0.1 | 0.1 | 0.0 | nil |
| 6-12 | 0 | 0 | 8.0 | 5.3 | 77.3 | 36.4 | 5.5 | 0.3 | 0.1 | 0.0 | t |
| Summer | | | | | | | | | | | |
| 0-6 | 0 | 0 | 2.0 | 1.2 | 67.6 | 15.1 | 4.6 | 0.2 | 0.1 | 0.1 | nil |
| 6-12 | 0 | 0 | 2.2 | 1.1 | 65.6 | 12.5 | 4.7 | 0.2 | 0.1 | 0.1 | nil |
| Fall | | | | | | | | | | | |
| 0-6 | 0 | 0 | 1.2 | 0.8 | 74.0 | 8.5 | 5.2 | 0.4 | 0.1 | 0.0 | nil |
| 6-12 | 0 | 0 | 6.0 | 3.9 | 63.6 | 13.2 | 4.9 | 0.4 | 0.1 | 0.0 | nil |
| 24-I | | | | | | | | | | | |
| Spring | | | | | | | | | | | |
| 0-6 | 0 | 0 | 10.4 | 5.6 | 109.6 | 38.4 | 6.5 | 0.1 | 0.1 | 0.1 | nil |
| 6-12 | 0 | 0 | 13.2 | 4.9 | 76.6 | 15.8 | 6.8 | 0.2 | 0.1 | 0.0 | nil |
| Summer | | | | | | | | | | | |
| 0-6 | 0 | 0 | 3.0 | 2.0 | 110.8 | 16.6 | 5.9 | 0.3 | 0.2 | 0.0 | nil |
| 6-12 | 0 | 0 | 4.6 | 0.9 | 107.6 | 10.8 | 6.2 | 0.4 | 0.2 | 0.1 | nil |
| Fall | | | | | | | | | | | |
| 0-6 | 0 | 0 | 6.4 | 1.7 | 109.0 | 16.4 | 6.2 | 0.2 | 0.2 | 0.1 | nil |
| 6-12 | 0 | 0 | 18.6 | 4.7 | 99.6 | 17.6 | 6.6 | 0.4 | 0.2 | 0.1 | Tr (M-) |
| 26-I | | | | | | | | | | | |
| Spring | | | | | | | | | | | |
| 0-6 | 0 | 0 | 1.6 | 0.9 | 70.4 | 18.6 | 6.3 | 0.2 | 0.1 | 0.0 | nil |
| 6-12 | 0 | 0 | 1.1 | 0.9 | 50.4 | 21.1 | 6.3 | 0.2 | 0.1 | 0.0 | nil |
| Summer | | | | | | | | | | | |
| 0-6 | 0 | 0 | 0 | 0 | 57.5 | 24.4 | 5.7 | 0.3 | 0.1 | 0.1 | nil |
| 6-12 | 0 | 0 | 0 | 0 | 73.6 | 49.2 | 5.8 | 0.2 | 0.2 | 0.0 | nil |
| Fall | | | | | | | | | | | |
| 0-6 | 0 | 0 | 0.4 | 0.8 | 96.4 | 22.9 | 5.7 | 0.2 | 0.2 | 0.0 | nil |
| 6-12 | 0 | 0 | 1.4 | 1.3 | 59.6 | 13.2 | 5.7 | 0.2 | 0.2 | 0.0 | nil |

* 0-6, 6-12 refer to soil depths in inches.

TABLE 16 Cont'd.

| | N | | P | | K | | pH | | Cond. | | Free Lime | |
|--------|-----------|----|-----------|-----|-----------|------|-----------|-----|-----------|-----|-----------|----|
| | \bar{x} | Sx | \bar{x} | Sx | \bar{x} | Sx | \bar{x} | Sx | \bar{x} | Sx | \bar{x} | Sx |
| 55-I | | | | | | | | | | | | |
| Spring | | | | | | | | | | | | |
| 0-6 | 0 | 0 | 0.8 | 0.8 | 62.2 | 20.2 | 6.6 | 0.1 | 0.1 | 0.1 | nil | |
| 6-12 | 0 | 0 | 1.9 | 1.8 | 55.8 | 20.4 | 6.8 | 0.5 | 0.1 | 0.1 | med. | |
| Summer | | | | | | | | | | | | |
| 0-6 | 0 | 0 | 0.4 | 0.6 | 71.2 | 14.9 | 6.1 | 0.1 | 0.2 | 0.0 | nil | |
| 6-12 | 0 | 0 | 1.3 | 0.6 | 76.4 | 26.2 | 6.6 | 0.4 | 0.3 | 0.1 | med. | |
| Fall | | | | | | | | | | | | |
| 0-6 | 0 | 0 | 0.2 | 0.5 | 72.2 | 30.5 | 6.2 | 0.3 | 0.2 | 0.1 | (L+) | |
| 6-12 | 0 | 0 | 0.6 | 0.9 | 85.4 | 19.5 | 6.5 | 0.7 | 0.3 | 0.7 | L-;M+ | |

of concentrating and cycling of nutrients in quantities which vary from one species to another. The work of Gagnon and Amiot (1958) shows that forest plants will concentrate nutrients in their leaves to the same extent on sites of different quality. This indicates that within certain tolerance limits, the forest plants can effect a redistribution of nutrients in an area ("reaction" *sensu* Clements¹) and eventually produce a mosaic pattern of nutrients which is partially dependent upon the distribution patterns of the species present. This nutrient mosaic may influence the distribution patterns of species which come later in a successional sequence.

Although I believe that the mineral nutrients and pH as measured may be relatively unimportant as controlling factors of the variability occurring within the pine vegetation, the fluctuations in the relative amounts of these factors can be related to the different forest types studied. It should be borne in mind when making comparisons between stands that although all were sampled at effectively the same calendar time, each stand was not at the same physiological state. For example, when the spring samples were collected, most plants in the three Jasper stands had broken morphological dormancy while in stand 47-B-I the soil 5 - 15 cm down was still frozen. Only plants like *Vaccinium scoparium* were seen to be just breaking dormancy. In stand 41-B-I the ground was not frozen but the plants were still dormant or just

¹Nature and structure of the climax. J. Ecol. 24: 252-284(1936)

breaking dormancy.

A. SEASONAL NUTRIENT FLUCTUATION

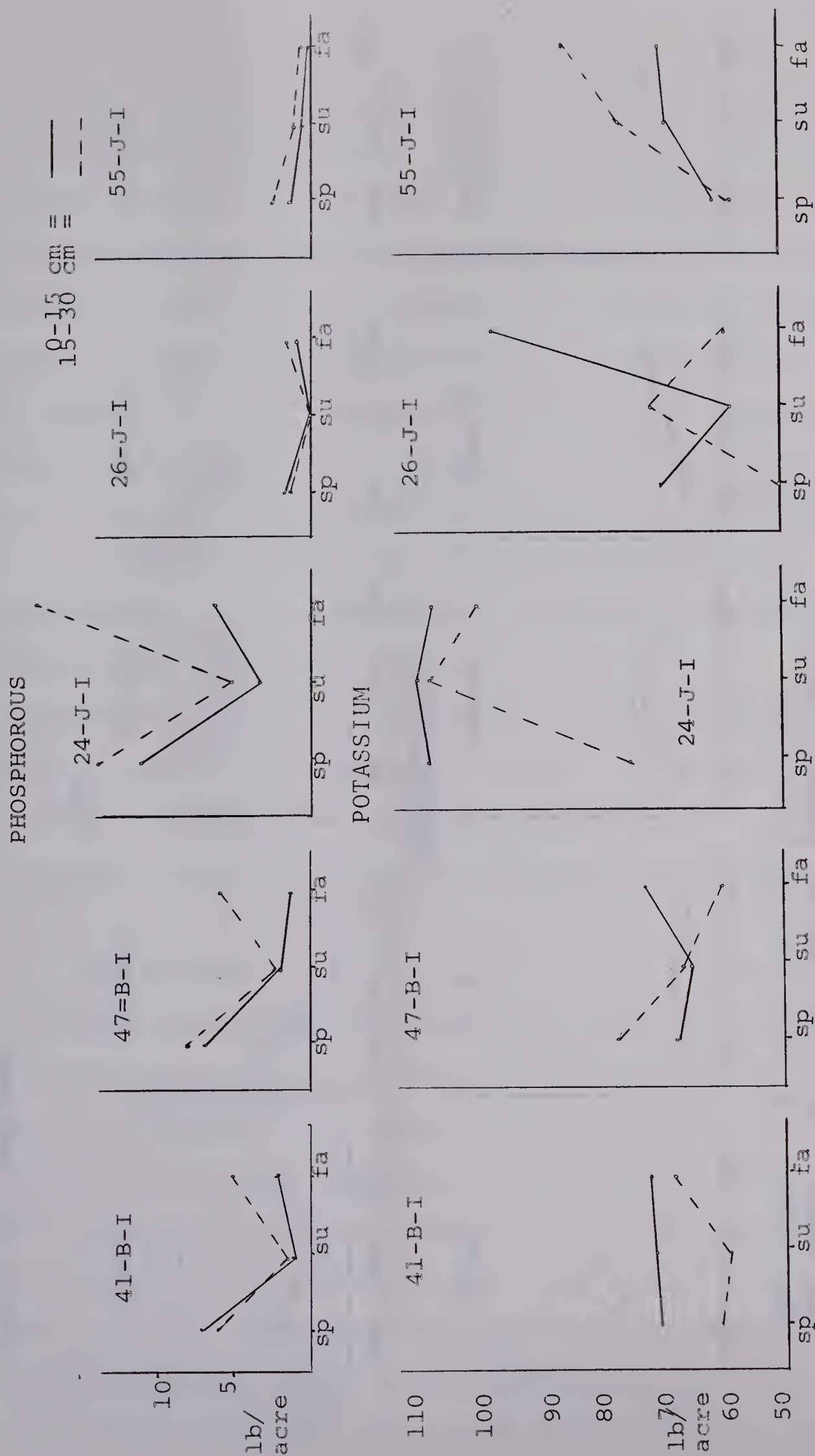
1. pH

The trend for all five stands was for pH's to decrease from spring to summer, then either increase or remain the same until autumn (see Fig. 227). This trend probably indicates an increase in decomposer activity during the warm, moist, early summer months with the concomitant drop in pH from the release of organic acids as decomposition products. In stands 24-J-I, 47-B-I, and 55-J-I, the surface 15 cm of soil was more acidic than the next 15 cm, probably because most decomposition is occurring in the thin humus layer present in these stands. Because there is only a thin to non-existent humus, the organic acids of decomposition must quickly be washed into the surface soil. In the case of 47-B-I and to a lesser extent in 55-J-I, the presence of free lime (CaCO_3) from Paleozoic carbonates in the lower horizon accounts for the near neutral pH of that horizon.

2. PHOSPHORUS

In all five stands there is a drop from late May to early September in the amount of measurable phosphates. The decrease in standard deviation (Table 16), concomitant with the drop in phosphate, indicates that sites of greatest phosphate utilization in each stand are probably those sites where phosphates were most abundant. The result is

FIGURE 227 SEASONAL VARIATION IN CERTAIN EDAPHIC FACTORS IN THE FIVE INTENSIVE STANDS.



that by mid summer, most sites have a uniformly low available phosphate concentration.

With the exception of stand 55-J-I, the amount of available phosphates then increased from August to September (Fig. 227). Paralleling this increase in phosphates is an increase in standard deviations of the mean P concentration (Table 16) indicating that accumulation of the phosphates is uneven within the intensive stands. Accumulation in late summer may be due to the fact that most plants have ceased active growth; thus phosphates released from decomposition of organic matter and parent material weathering would equal or surpass uptake.

Stands 26-J-I and 55-J-I had very small quantities of phosphates at the three sampling periods. Supply of phosphates may be an important limiting factor in these two stands especially in 26-J-I where no measurable amounts were found in the August samples.

3. POTASSIUM

The observed seasonal fluctuation in available potassium is not consistent in all five stands (see Fig. 227). In the three Jasper stands there is a large increase in the amount of available potassium in the 15-30 cm soil horizon, possibly due to the combined effects of leaching and release from decomposition being greater than plant uptake (*i.e.* K is abundant). The drop in the amount of measurable potassium in the upper 15 cm of soil in stand 26-J-I, combined with the high precipitation there,

supports the leaching hypothesis.

In stand 41-B-I, K decreases from spring to summer in the lower horizon. This could possibly be due to heavy utilization by *Menziesia* in addition to very active leaching due to high precipitation in the region and steep slope on which the stand is situated. The late summer increase in K in the surface horizon may be due to release from decomposition and weathering exceeding utilization. Precipitation is also less during this period. In stand 47-B-I surface K concentrations remained constant indicating a steady state between supply, utilization, and loss. The increase in K in the lower horizon in late summer might indicate lower utilization and therefore permit accumulation from weathering and leaching.

It appears that large amounts of potassium were being made available in the surface 15 cm of soil, in stands 26-J-I, 41-B-I and 55-J-I, either from the processes of decomposition of organic matter or from weathering of parent materials, or both. For example, note the relatively large increases in potassium in the upper 15 cm of soil from August to September in stands 41-B-I and 26-J-I, and the steady increase throughout the season in stand 55-J-I.

4. CONDUCTIVITY

There was an increase in conductivity from May to August in all stands except 47-B-I (Fig. 227). From August to September there was either a decrease or a

levelling off of conductivity values. This indicates a tendency for an increase in salt concentration throughout the early part of the growing season. Salts from the weathering of parent materials and the release of salts from the decomposition of organic matter in excess of that utilized by the plant community, probably accounts for the increased conductivity.

The large decrease in conductivity in stand 47-B-I may be due to the excessive leaching of the soil because of its coarseness and porosity plus the very high precipitation received there (Fig. 7).

In general it appears that build-up of plant nutrients (*e.g.* potassium and phosphorous) occurs primarily in the late summer and early autumn when uptake is low and yet temperatures are high enough for decomposition to occur. The period of greatest utilization of nutrients by plants appears to be during the spring and early summer, *i.e.* when most active growth is occurring. Decomposition of organic matter is probably most rapid during the same period when temperatures are high and moisture fairly abundant, but because of rapid uptake, there is a net drop in the quantity of soil nutrients available to plants during this period.

B. DESCRIPTION AND IDENTIFICATION OF SOILS

The geological parent material of the soils of the sampled pine forests of Banff and Jasper are derived

mainly from Precambrian and Lower Cambrian quartzites and sandstones, and Upper and Lower Paleozoic limestones and dolomites. Some Triassic siltstones occur to the south of Banff townsite. The geologic material occurs primarily in the form of glacial drift and alluvial deposits of considerable but undetermined depth overlying bedrock in the valley bottoms. Glacial drift, colluvium, and weathered bed rock form the parent material for soil on the valley walls (personal communication with Dr. H.A.K. Charlesworth, Department of Geology, University of Alberta).

The widespread occurrence of carbonates in the Parks is largely responsible for the high soil pH's recorded. The average pH of the humus is 5.0, while that of the upper 15 cm of mineral soil is 6.5 and that of the next 15 cm of soil is 7.0.

Identification of the soils of the pine forests in Banff and Jasper is difficult because of the lack of information regarding the mountain soils of Alberta. A very tentative identification of the soils in this study is presented in Table 17. This classification is based upon:

1. textural analysis of horizons
2. colour of horizons
3. the assumption that many of the soils in the Parks are similar to soils described from the Hinton area east of Jasper.

In the Hinton area, soils of pine forests often have bright red B horizons which, however, do not have high iron

TABLE 17. SOILS IDENTIFICATION

| Stand # | Classification | pH | Diagnostic horizon | | Classification | pH | Diagnostic horizon |
|---------|----------------|-----|--------------------|---------------------------|------------------------------|-----|--------------------|
| 41 | DEB | 6.0 | Bm | 1 | OR | | |
| 42 | DEB | 6.6 | Bm | 2 | OEB | 7.9 | Bm |
| 40 | DEB? | 5.8 | Bm | 3 | DEB | 7.0 | Bm |
| | | | | 16 | DEB | 6.7 | Bm |
| 25 | DEB | 6.0 | Bm | 24 | DEB | 7.0 | Bm |
| 28 | DEB | 6.5 | Bm | 27 | DEB | 6.7 | Bm |
| 31 | DEB | 6.4 | Bm | 30 | DEB | 6.8 | Bm |
| 33 | DEB | 7.2 | Bm | 32 | OEB | 6.6 | Bm |
| | | | | 35 | DEB | 6.6 | Bm |
| 26 | DEB | 6.6 | Bm | | | | |
| 18 | DEB | 5.7 | Bm | 38 | ? | | |
| 17 | DEB | 6.3 | Bm | 37 | DEB | 6.7 | Bm |
| 7 | DEB | 7.0 | Bm | 21 | DEB | 6.2 | Bm |
| 11 | DEB | 6.8 | Bm | 54 | OGL | 7.9 | Bt |
| 12 | OGL | 6.3 | Bt | 53 | OGL | 6.5 | Bt |
| 9 | LR | | | 4 | OEB | 6.5 | Bm |
| 44 | DEB | 6.5 | Bm | 8 | OEB | 7.4 | Bm |
| 43 | DEB | 6.9 | Bm | 22 | OGL | 7.2 | Bm |
| 48 | OGL | 6.9 | Bt | 6 | OEB? | 7.2 | Bm |
| 51 | DEB (DDB) | 5.6 | Bm | | | | |
| | | | | 23 | OGL | 7.3 | Bt |
| 47 | DEB | 7.3 | Bm | 61 | OR | | |
| 39 | OEB or OGL? | | | 34 | OGL | 7.6 | Bt |
| 10 | DEB | 6.3 | Bm | 56 | OEB | 6.8 | Bm |
| 45 | DEB | 7.0 | Bm | 63 | OR | | |
| | | | | 62 | OR | | |
| 49 | OR | | | 15 | DEB | 6.2 | Bm |
| 57 | Brunisol | 7.5 | Bm | | | | |
| 58 | OGL | 6.2 | Bt | | | | |
| 59 | DEB | 6.5 | Bm | | | | |
| 60 | DEB | 5.9 | Bm | | | | |
| | | | | Note: LR - lithic regosol | | | |
| 46 | DEB | 7.4 | | | OR - orthic regosol | | |
| 36 | DEB (DDB) | 5.0 | Bm | | | | |
| 14 | OGL | 6.9 | Bt | | DEB - degraded eutric | | |
| 50 | OGL (OEB) | | | | brunisol | | |
| 13 | LR | | | | DDB - degraded dystic | | |
| 20 | EB(?) | | | | brunisol | | |
| 55 | OGL | 7.1 | Bt | | OEB - orthic eutric brunisol | | |
| 52 | OEB | 6.0 | Bm | | | | |
| 19 | OGL (?) | | | | OGL - orthic gray luvisol | | |
| 29 | OGL | 7.4 | Bt | | | | |
| 5 | gleyed EB | 7.2 | Bm | | | | |

and aluminum content and thus do not meet the specifications of a B_f horizon (personal communication, Dr. D. J. Pluth, Department of Soil Science, University of Alberta). These soils, therefore, are not Podzols but either Brunisols or Luvisols depending upon how much clay is present in the B horizon relative to the A horizon. To be classified as a Luvisol, the solum must have a diagnostic B_t horizon which is defined in the Canadian soil classification system (Proceedings of the Seventh Meeting of the National Soil Survey Committee of Canada, 1969) as follows:

1. if there is less than 15% clay in the B, then there must be at least 3% more clay in the B than in the A horizon;
2. if there is between 15% and 40% clay in the B, then the ratio of clay in the B to that in the A must exceed 1.2;
3. if there is more than 40% clay in the B, then there must be greater than 8% more clay in the B than in the A horizon.

If a soil was found not to have a B_t horizon, then the B was called a B_m and thus the soil was identified in the Brunisolic Order with the exception of a few soils identified as Regosols. Most of the soils classed as Brunisols probably belong to the Eutric Great Group because the B_m horizon has a pH greater than 5.5. The base saturation of the B_m is an important criterion in the distinction of Great Groups in the Brunisolic Order. Therefore, base

saturation will have to be determined before the Great Group can be known with certainty. However, Eutric Brunisols usually have pH's greater than 5.5 (B_m horizon), thus most of the Brunisols beneath pine in the Parks will be in the Eutric Great Group.

If the soils are Eutric Brunisols, then most of them are probably of the Degraded subgroup because of the presence of an A_e horizon. If such an eluviated horizon is absent, then the soil is probably an Orthic Eutric Brunisol.

There does not appear to be any strong correlation between forest type and soil type as shown in Table 17, but 10 of the 13 Orthic Gray Luvisols occur in the Mesophytic Forest Class and the remaining three occur in the Moist Class. The environment of forests in the Xerophytic Class may be too dry for active soil formation while in the Moist Class the temperatures may be too low for active soil genesis. Therefore, it is primarily in the Mesophytic Forest Class that conditions have favoured formation of a B_t horizon.

An attempt was made to correlate attributes of the pine populations of Banff and Jasper with edaphic factors ("r" coefficients in Table 18). Only pH of the humus shows a statistically significant, although low, correlation with some tree attributes and stand elevation. The correlation between humus pH and tree attributes seems reasonable since the nature of the vegetation has a strong bearing upon the humus it creates.

TABLE 18. CORRELATION COEFFICIENTS BETWEEN ATTRIBUTES OF STANDS OF PRIMARY SURVEY AND EDAPHIC FACTORS (correlations have been multiplied by 100)

| VARIABLES | 1* | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|-----------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 2. Maximum tree height | +91 | | | | | | | | | | | | | | | | |
| 3. Average crown depth | +75 | +70 | | | | | | | | | | | | | | | |
| 4. Maximum crown depth | +66 | +68 | +93 | | | | | | | | | | | | | | |
| 5. Average basal area | +06 | +04 | -34 | -33 | | | | | | | | | | | | | |
| 6. Tree density | -63 | -59 | -62 | -56 | +07 | | | | | | | | | | | | |
| 7. Maximum stand age | +12 | +12 | -03 | -05 | -09 | +19 | | | | | | | | | | | |
| 8. Tree population age | +49 | +45 | +18 | +12 | +25 | -32 | +31 | | | | | | | | | | |
| 9. Tree population-diameter | +75 | +68 | +73 | +62 | -17 | -70 | +03 | +48 | | | | | | | | | |
| 10. Stand elevation | -20 | -20 | -32 | -33 | +36 | +01 | -19 | +05 | -07 | | | | | | | | |
| 11. P surface | -11 | -21 | -13 | -21 | +11 | -01 | -12 | -07 | -12 | -14 | | | | | | | |
| 12. P subsurface | -18 | -20 | -13 | -15 | +02 | +03 | -16 | -17 | -03 | +11 | +46 | | | | | | |
| 13. K surface | -02 | -07 | +02 | +03 | +15 | +08 | -07 | -18 | -28 | -17 | +21 | +17 | | | | | |
| 14. K subsurface | +04 | +03 | -01 | -06 | +16 | -16 | -18 | -14 | -17 | -03 | +43 | +41 | +50 | | | | |
| 15. Conductivity surface | +05 | -06 | +16 | +08 | +10 | -04 | +05 | +10 | -03 | +10 | +5 | -08 | +35 | +30 | | | |
| 16. Conductivity subsurface | -03 | -13 | -05 | -15 | +20 | -08 | -10 | +07 | -09 | +25 | +02 | -06 | +29 | +35 | +62 | | |
| 17. Na surface | -05 | -04 | -24 | -26 | +17 | +02 | +15 | -06 | -21 | -13 | +11 | +11 | +17 | +19 | -07 | -02 | |
| 18. Na subsurface | +01 | -08 | -09 | -16 | +11 | -03 | +01 | +03 | -16 | -11 | +22 | +10 | +29 | +42 | +21 | +49 | +47 |

* 1. Average tree height

5% level of significance = 23

TABLE 18. Cont'd.

| VARIABLES | 1 * | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|-----------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 2. Maximum tree height | +91 | | | | | | | | | | | | | | | |
| 3. Average crown depth | +75 | +66 | | | | | | | | | | | | | | |
| 4. Maximum crown depth | +67 | +66 | +93 | | | | | | | | | | | | | |
| 5. Average basal area | +09 | +08 | -30 | -28 | | | | | | | | | | | | |
| 6. Tree density | -62 | -58 | -63 | -57 | +07 | | | | | | | | | | | |
| 7. Maximum stand age | +07 | +07 | -08 | -12 | -07 | +20 | | | | | | | | | | |
| 8. Tree population age | +48 | +45 | +17 | +10 | +28 | -35 | +25 | | | | | | | | | |
| 9. Tree population-diameter | +73 | +67 | +75 | +65 | -17 | -71 | -01 | +46 | | | | | | | | |
| 10. Stand elevation | -17 | -16 | -26 | -28 | +32 | -03 | -17 | +08 | -04 | | | | | | | |
| 11. pH surface | -03 | -06 | +11 | +16 | -05 | -11 | -13 | +01 | -10 | +08 | | | | | | |
| 12. pH subsurface | +06 | +07 | +21 | +20 | -06 | -09 | -13 | +02 | -06 | +14 | +66 | | | | | |
| 13. Nitrogen in humus | -10 | -07 | -24 | -16 | +15 | +11 | +13 | -08 | -21 | -05 | -07 | -20 | | | | |
| 14. P in humus | -15 | -27 | -10 | -12 | +25 | +16 | -24 | -17 | -25 | -02 | +07 | -14 | +10 | | | |
| 15. K in humus | -09 | -14 | -22 | -18 | +28 | +15 | +01 | -05 | -29 | -05 | +26 | +05 | +30 | +62 | | |
| 16. pH of humus | +21 | +23 | +40 | +46 | -32 | -31 | -01 | -02 | +15 | -35 | +55 | +44 | -05 | -01 | +14 | |
| 17. Conductivity of humus | +01 | -00 | +12 | +15 | -05 | +06 | +06 | -04 | -15 | -10 | +46 | +38 | -05 | +37 | +53 | +59 |

* 1. Average tree height

The trend for lower pH's in the humus at higher elevations is probably due to several factors, *eg.* greater precipitation at higher elevations would tend to leach carbonates away from the surface and thus permit the build-up of a more acidic humus, or the cooler temperatures at higher elevations might favour the accumulation of organic acids as the major products of decomposition.

Humus pH was found to decrease with increasing basal area. If higher basal areas indicate greater growth potentials, then it would be expected that the more productive sites would produce trees with more needles. The more coniferous needles that go to make up the humus the more acidic that humus will probably be.

That humus pH's tend to decrease with increasing tree density might indicate that (within limits) with more trees there is more pine needle litter which gives rise to an acidic humus upon decomposition. The trend for higher humus pH's in stands with trees which have deeper crowns is correlated with the density-pH relationship in that the less dense the stand, the deeper are the tree crowns. These correlations are so low that very little significance can be attributed to them at present.

The preceding two paragraphs are largely speculative in nature. The ecological significance of the low correlations cited is not certain. That the forest types described are strongly correlated with elevation may bear some relation to the humus pH-elevation relationship cited,

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but humus pH by itself does not correlate strongly with forest types (exceptions may be the *Menziesia* and *Vaccinium* types [Table 17] but the number of samples is small). The very low correlation coefficients between attributes of the pine population and the edaphic factors measured indicate clearly that the primary causes of variability in the pine forests of the two Parks include factors other than those relating directly to the soil.

XII. PRECIPITATION

The importance of water to the development of pine forests in the two Parks has been stressed many times in the preceding section. Field observations indicated that there were definite patterns to rain storms--certain areas were in apparent rain shadows while others were frequently crossed by storms. Thus I considered it unwise to interpolate the quantity of rain received at a given intensive site from the precipitation data available for the Banff, Lake Louise, and Jasper townsites.

Measurements for several years at many sites would be necessary before accurate determinations of rainfall patterns could be made. Nevertheless, I wished to determine whether one summer's sampling would show any significant differences between sites. The very crude estimates of precipitation obtained within the intensively studied forest sites (see Fig. 7) do show differences

which tend to agree with the subjective evaluation of "moistness" of the stands.

The differences in precipitation between Banff and Jasper townsites for the summer of 1968 were slight. At both townsites there was more precipitation in the first part of the season than in the second which may be due to a greater frequency of thunderstorms in the late spring and early summer than in the latter part of the season.

The two Banff stands recorded more rain in the early part of the season than did Banff townsite for the same period. Local storms of a convectional and orographic nature could account for the observed differences. During the latter part of the season, however, both of the stands and the townsite recorded similar amounts of rain indicating that regional or cyclonic storms were responsible for most precipitation during that period.

The situation in Jasper is somewhat different. Stand 55-J-I received more rain during both sampling periods than did Jasper town thus indicating the greater occurrence of local storms for a longer period of time in the vicinity of stand 55-J-I. Both stands 26-J-I and 24-J-I, but especially the latter, received less rain than Jasper town during the first sampling period. This indicates the frequency of local storms which come down the Miette River valley. Jasper town recorded less rain, however, for the latter part of the season than did stands 26-J-I and 24-J-I. It is notable that stand 24-J-I received less rain

in both sampling periods than did any of the other four Intensive Stands. This supports the xeric classification of stand 24-J-I.

Long term, more detailed studies of precipitation patterns in these Parks would greatly add to our understanding of the vegetation which appears to be so dependent upon the supply of water.

XIII. INTEGRATION AND DISCUSSION

Pinus contorta-dominated vegetation of Banff and Jasper occupies sites from the upper montane zone to the high sub-alpine zone. The former zone is warm and dry and is characterized by the presence and abundance of *Pseudotsuga menziesii* on the lower slopes and bottoms of the major valleys. The latter zone is generally cool and moist and dominated by *Picea-Abies* forests. *Pinus* is a common component of some high subalpine *Picea-Abies* forests (Beil 1966) and also of montane *Pseudotsuga* forests (Stringer 1966). Pure stands of pine may occur in both areas, even to timber line in the sub-alpine (personal field observations). In both zones, pure stands of pine are usually the result of fire.

Pinus contorta is a seral dominant in Banff and Jasper as it is over most of its range in North America. In some areas such as the Sierra Nevada (Klyver 1931) and "near the northern limit of its distribution" (Shelford 1963), *Pinus contorta* appears as the dominant or co-dominant of the climax community. Stands such as 55-J and 24-J may represent a type of physiographic pine climax in Jasper.

The rugged mountain terrain of the two Parks offers a wide range of *Pinus contorta* habitats. Such habitat diversity results in very different understory vegetation. The classification of forest types in this thesis is based upon the premise that the variations in the understory vegetation are correlated with habitat differences which are not readily discernible from a study of the tree stratum alone.

In general, it appears that the availability of water is the single, dominant, controlling factor in determining the major characteristics of the understory vegetation. To refer, though, to water availability as a single factor is to greatly oversimplify the situation. Water availability is itself determined by a large complex of factors of which only a few were studied for this thesis. Some of the factors affecting water availability are: (1) precipitation--its amount, form and time of occurrence; (2) soil characteristics such as textural composition, stoniness, hardpan formation; (3) evapotranspiration which is affected by heat, radiation balance, density and type of vegetation cover, and topographic location; (4) ground water supply; and other factors. The various combinations in which these factors occur and the degree to which they are expressed are important in determining the water balance and character of the vegetation at any particular site.

The Primary Survey has permitted the description of three main moisture classes and eight forest types (*sensu* Cajander 1926) dominated by pine. The description has resulted in the following classification based upon floristic and physiognomic similarities and differences between stands:

A. Moist Class:

1. *Menziesia glabella* type (MG)
2. *Vaccinium scoparium* type (VS)
3. Feather Moss type (FM)
4. *Alnus crispa* type (AC)

B. Mesophytic Class:

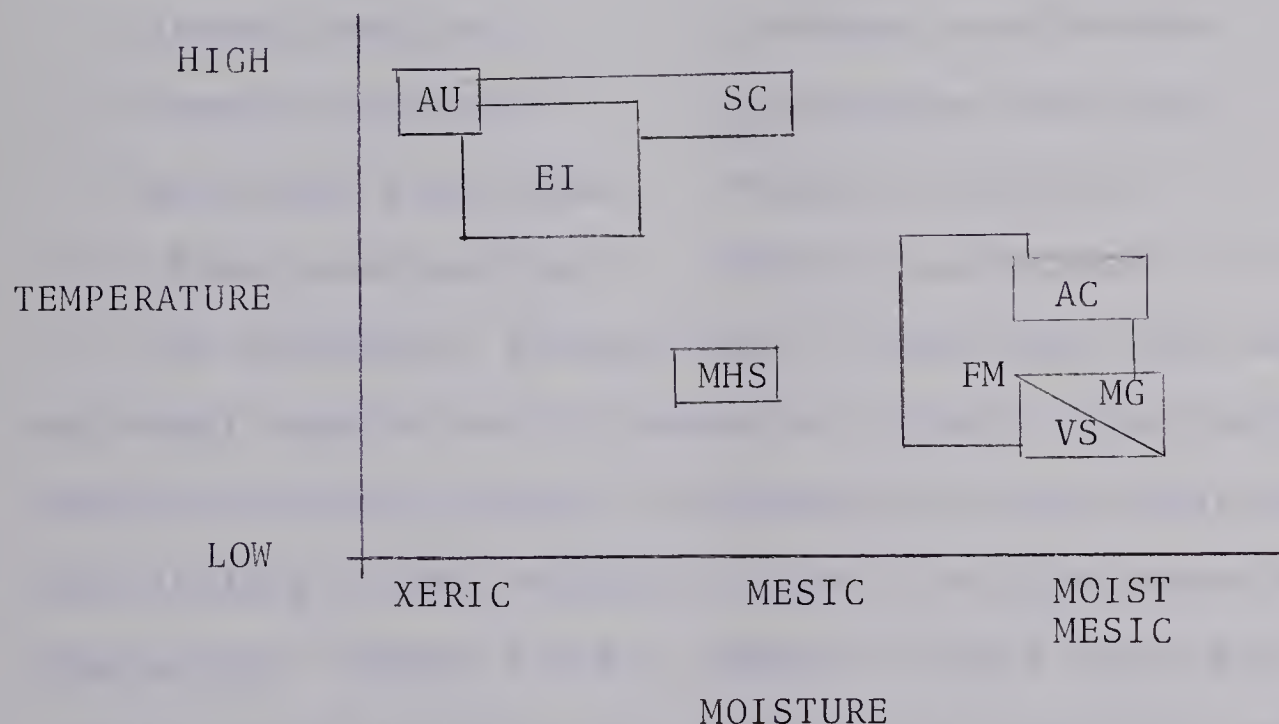
1. *Shepherdia canadensis* type (SC)
2. Mesic High Subalpine type (MHS)
3. *Elymus innovatus* type (EI)

C. Xerophytic Class:

1. *Arctostaphylos uva-ursi* type (AU)

The forest types may be arranged in a series (Fig. 228) similar to Sukachev's Ecological Series (1928).

FIGURE 228. TEMPERATURE AND MOISTURE RELATIONSHIPS OF FOREST TYPES.



In general the Moist Class occurs at higher elevations than the Mesophytic Class which occurs higher than the Xerophytic Class, but exceptions do exist where particular habitat factors permit. For example, the Feather Moss type will occur at low elevations as in stand 26-J-I.

The three Forest Classes are not strongly different in floristic composition, but there are certain species, which by themselves and in combination with other species, may be considered more characteristic of one of the Classes than of the others (Braun-Blanquet 1932). The moist forests are generally of moderate to high density and have closed tree canopies. The ground is usually covered by *Hylocomium*, *Pleurozium*, and some *Ptilium*, but exceptions do occur such as the *Menziesia* type with a poor bryoid stratum. The following species are all associated with moister sites in the pine communities:

| | |
|-----------------------------|-----------------------------|
| <i>Arnica cordifolia</i> | <i>Lonicera involucrata</i> |
| <i>Cornus canadensis</i> | <i>Lycopodium annotinum</i> |
| <i>Equisetum scirpoides</i> | <i>Menziesia glabella</i> |
| <i>Ledum groenlandicum</i> | <i>Pyrola asarifolia</i> |

The xerophytic forests tend to have open tree canopies and small populations of understory plants. Many of these areas are heavily grazed and browsed by large herbivores thus contributing to the xerophytic aspect and sparseness of the vegetation. Shrubs are not common in these areas but a few widely spaced individuals of *Shepherdia canadensis* and *Juniperus communis* of no great vigour may be found. *Rosa acicularis* and *Amelanchier alnifolia* occur as dwarfed plants 15-25 cm tall. *Arctostaphylos uva-ursi* is the single, very abundant understory species, although *Antennaria rosea*, *nitida*, *Senecio cymbalarioides* (Jasper), *Festuca scabrella*, *Festuca saximontana*, *Cladonia pyxidata* and *Peltigera canina*

even if not generally abundant are indicative of dry habitats.

Between the moist and xerophytic forests are the mesophytic ones where shrubs like *Juniperus* and *Shepherdia* reach their greatest abundance and vitality. Stands in this type of habitat are usually of moderate tree density. Species such as *Antennaria racemosa*, *Antennaria neglecta*, *Achillea millefolium*, *Aster ciliolatus*, and *Senecio aureus* are abundant.

The *Elymus innovatus* type appears to occupy intermediate positions on a moisture gradient between the *Arctostaphylos* and *Shepherdia* types. The *Elymus* type may occur on cooler sites than either of the other two types. The *Shepherdia* and *Arctostaphylos* types were seen to grade directly into one another, sometimes with and sometimes without a transition zones where *Elymus* was very abundant. It is not certain what factors control the occurrence of the *Elymus* type.

The tentative classification of the *Pinus contorta* vegetation was successfully tested and its validity strengthened by analyzing the Primary Survey species-cover data by means of a Cluster Analysis. The results of this analysis elucidated some of the environmental relationships between the forest types and also aided in assigning stands to particular types.

The method of Cluster Analysis produced a hierarchical classification of the pine vegetation. The basis of the hierarchy is the degree of similarity between stands. At the lowest levels only those stands which are very similar

are grouped in the same cluster. At higher levels, more variability (*i.e.* greater dissimilarity) between stands is permitted within clusters. By comparing the clusters formed at different levels in the Cluster Analysis, the inter-relationships of the clusters can be determined.

The mechanics of Cluster Analysis inherently impose discreteness upon the data being analyzed, whereas the method of ordination emphasizes continuity. In this study, the continuous nature of the results of the ordination yielded very complex patterns of forest types on the ordination fields. In view of the success obtained with the Cluster Analysis, the ordination results were considered to obscure to warrant further study at this time. The complexity of the ordination may be the result of the very low average similarity (0.24) between stands, in conjunction with a large number of significant dimensions in the data. The Factor Analysis (see p. 29) indicated 12 significant factors (*i.e.* dimensions). Since the primary value of ordination lies in its ability to visually represent relationships in two or at most three dimensions, the distortions arising from representing 12 dimensions in less than four resulted in an array of stands which, although it could be interpreted in terms of the available information, of itself added no appreciable new information or insight concerning the pine vegetation. It only indicated (1) that the situation was very complex and (2) that a "moist" group could be distinguished from the rest of the stands.

Vegetation units of the forest types described in this thesis were not easily recognized in the ordination results.

Since most of the pine communities in the Parks are seral, and therefore, by definition are not in equilibrium with their environment, it is possible that vegetationally different pine stands could occupy similar sites and also that the same type of pine community could occupy different sites (personal communication with Dr. G. H. La Roi, Department of Botany, University of Alberta). It is not certain to what degree this unstable nature of a seral community will affect its representation in an ordination.

The Index of Similarity used in the ordination was that proposed by Czekanowski (1913). Austin and Orloci (1966) have shown that this index does not yield results which are accurately representable in the Euclidean space of an ordination. But because there are usually three or fewer dominant factors controlling the relationships between stands, the distortion which results from representing stands relationships in less than four dimensions is small. It is uncertain how significant this relationship is between Czekanowski's coefficient and Euclidean space relative to the failure of ordination as attempted in this study.

Cluster Analysis circumvents the problem of multi-dimensionality by not presenting the results in terms of two or three dimensional space. The analysis simply indicates that particular stands have a closer similarity between themselves than with other groups or stands. Much information

is lost in this kind of simplification but the loss is well compensated for by the gain in the understanding of the underlying order and relationships which exist between stands.

A second Cluster Analysis of the Primary Survey was made but not reported above. This latter analysis differed from the first in that the cover scale used in calculating the Indices of Similarity was: 0.1, 0.5, 1, 2, 3, 4, 5, 6 instead of the cover-class mid-points, *i.e.* (0.1), 0.5, 2.5, 10, 20, 37.5, 67.5, 87.5. The main result of the second analysis is the same as the first, thus providing strong evidence for the existence of the forest types as described. What was significantly different about the second Cluster Analysis was the order in which stands were admitted to clusters. The use of the 1-6 scale results in greater emphasis on floristic similarities based upon the presence or absence of species than upon the quantitative similarities and differences of species populations between stands. The importance of species which are merely present (or rare) is increased in the second analysis, by the relatively greater quantitative estimate of their cover. During the clustering procedure, then, stands which are floristically similar are brought together early even if they differed somewhat in the quantity of the species present. Because stands which are geographically close together tend to have the same species present, the second Cluster Analysis emphasizes geographic relationships while the first emphasizes similarities in species abundance between stands.

The first type of analysis therefore probably represents more accurately a classification based upon vegetational and ecological similarities while the second analysis emphasizes floristic similarity.

The purpose of classifying the pine vegetation of the two parks may be summarized as follows: (1) to both illustrate and describe habitats in which *Pinus contorta* is the dominant species, and (2) to describe phases of the pine vegetation which will facilitate the description of the relationships between the pine vegetation and other vegetation types in the two Parks.

As is evident from the classification presented on page 13, both floristics and physiognomy are major criteria. Differences in both species composition and community structure between stands indicate differences in the habitats of the stands. Gause's Principle (Odum 1959) of one species to one niche forms the theoretical basis for using floristic criteria as indicators of habitat. The use of physiognomy as an indicator of habitat is not as widely accepted as is Gause's Principle but both Oosting (1956) and Cain (1950) indicate that differences in physiognomy between areas can be indicative of differences ~~can be indicative of differences~~ in climate or microhabitat. Kùchler (1967) has made extensive use of physiognomy in vegetation mapping and classification.

None of the forest types in the three forest classes

was found to be restricted to one of the Parks even though examples from the Primary Survey may come from only one Park. My own field observations have indicated, for example, that both the *Menziesia* and *Vaccinium scoparium* types occur in Jasper as well as Banff and that the *Alnus* type also occurs in Banff.

Although no effort was made to determine the areal extent of each forest type in each Park, certain geographic differences in abundance of the types did become evident during the course of this study. (1) The *Arctostaphylos uva-ursi* type is much more extensive in Jasper than in Banff. The pine savanna between Henry House and Devona in Jasper is indicative of xerophytic conditions that are not found in Banff. (2) The *Shepherdia* type is also present in both Parks, but is represented by a relatively dry phase in Jasper compared with Banff. As described on page 79 the vegetation of the Banff *Shepherdia* type stands has a greater species diversity and is more lush than the Jasper representatives of this type. (3) The pine stands of Jasper may have a higher average cover than those of Banff. Stringer (1966) however, reported higher cover values in the Banff *Pseudotsuga* stands than in the Jasper stands.

The *Elymus* type of pine forest is of especial interest relative to the *Pseudotsuga* vegetation of the two Parks. Stringer (1966) described a *Pseudotsuga/Elymus* association as being representative of old, mature stands of *Pseudotsuga*

which had a dense, closed tree canopy. Stringer hypothesized that the *Elymus* might have a competitive advantage over other species in a habitat of low light such as exists in these mature *Pseudotsuga* forests. The *Pseudotsuga/Elymus* association does not appear to be closely related to the *Elymus* type of pine forest described in this thesis. The modal representatives of the *Elymus* type had well-developed herb strata, especially in stand 4-B. This seems in strong contrast to the generally poorly developed herb stratum of the *Pseudotsuga/Elymus* association. No evidence was found to suggest that *Pseudotsuga* would succeed the *Pinus* on these sites.

Without exception, the pine forests included in this study have become established following fire, and although all areas of pine in the two Parks were not studied, it is quite unlikely that any fairly pure stands of pine in these Parks have not resulted from a previous fire. The constant occurrence of fire in the history of *Pinus contorta* in the two Parks is in accordance with the observations of Smithers (1961) for the foothills of western Alberta.

Stand 24-J-I has a two-aged pine tree stratum. In the description of the tree stratum of this stand (p. 201) an interpretation of the pine age structure is given. It is based upon the differential burning of dense and open areas of trees. A similar phenomenon has been described by Dowding (1929) in *Pinus banksiana* vegetation on sandhills near Cookville, Alberta. She reported that fires are

relatively ineffectual in the scant vegetation of open pine woods but that areas of denser tree growth have been repeatedly destroyed by fires.

No concerted effort was made to determine the details of the fire history of the two Parks. It appears though that fires occur much more frequently in the warm, dry bottoms of the major valleys than they do in cooler, moister situations at higher elevations in or near certain smaller side valleys. The lack of deadfall of pre-fire trees in the warm, dry stands is in sharp contrast to the thick tangle of fallen trees of the pre-fire forests on cool, moist sites. The deadfall in the drier sites appears to have been consumed by ground fires which occurred after the main forest fires (see p. 207).

Because most of the stands of this study were not situated near the railways, the age data available can neither contest nor corroborate Stringer's 1966 observation that numerous forest fires occurred in Banff as a result of the 1880-1890 period of railway construction.

Most of the pine forests of the two Parks may be described as being "even-aged". By even-aged is meant that the majority of the ages of the present trees are similar. Most stands, however, have an absolute range of ages of about 30 years. Horton (1953 and 1955) has reported lodgepole pine seedling establishment as taking about six years following fire with only a small amount after this period, and D. T. Mason (1915) reports 91% of

lodgepole reproduction becoming established within 10 years following fire and the remaining 9% coming in over the next 20 years. Thus on the average, the *Pinus contorta* forests of Banff and Jasper become established about as quickly as the pine forests in the foothills to the east and south.

Arceuthobium americanum (dwarf mistletoe) occurs sporadically in both Banff and Jasper with infection appearing more extensive in Jasper and particularly in the vicinity of Jasper townsite. Infection appears heaviest in the lower valley areas but is not restricted there. Stands which were most severely infected (17-J, 32-J, 53-J, and 57-J) usually had relict trees present, *i.e.* trees which were not killed by the last fire. These relict trees were often heavily infected and as Gill and Hawksworth (1964) stated, probably serve as sources of infection for the present stand. It should not be misconstrued, however, that all old trees are sources of *Arceuthobium* infection. This was not found to be the case in either Park.

The general relationship between elevation and latitude with respect to vegetation types is well known (Good 1964, Daubenmire 1943). There does not appear to be any agreement yet as to a quantitative description of the relationship. Hopkins (1938) proposed a compensation of 100 ft per 15 minutes of latitude. By comparing the elevations of forest types which were studied in both Parks (*i.e.* the *Shepherdia* and Feather Moss types) it is evident that the compensation in elevation for changes in latitude in this area should be closer to 200 ft per

15 minutes. This latter compensation factor agrees with that suggested by Stringer (1966) for the *Pseudotsuga* vegetation of Banff and Jasper.

The general successional status of the pine forests of Banff and Jasper is that of a seral community which becomes established following forest fires and is eventually succeeded by a *Picea-Abies* dominated community. This successional sequence appears to be true for all moist-to-mesic areas such as occur at higher elevations and in and near certain moist side valleys. Such a sequence is in accordance with the observations of others *e.g.* Lewis, Dowding and Moss (1928), Cormack (1953) and Smithers (1961) for the foothills region of Alberta. It would seem, though, that the pine does not completely disappear from the climax community but rather becomes a subordinate species in a climax, mixed-coniferous forest (Beil 1966).

For pine to maintain even a small population in a climax forest it must be able to reproduce. Although specific work regarding pine reproduction in climax forests was not done for this thesis, the following observations are pertinent. In the description of the tree stratum of stand 26-J-I (p. 166) it was noted that the present pine forest is mature, tending towards senescence, and contains a significant amount of pine regeneration. Since pine is a shade intolerant species, it may be concluded that the young pine are maintaining themselves because of the large degree of canopy opening resulting

from the windthrow of old, dead trees. D. T. Mason (1915) has described pine reproduction occurring beneath canopy openings resulting from the falling of old pines in Montana. Thus it would appear that a "gap phase" replacement (Watt 1947) of pine can occur under certain circumstances.

It was not possible to clearly ascertain or describe the successional status of two of the five Intensive Stands (55-J-I and 24-J-I). Both of these stands occur in warm dry areas which are prone to fires and where reproduction of *Picea* and *Abies* is not abundant if present at all. The development of these stands to a typical climax may be dependent upon the occurrence of a series of years with above-average precipitation coinciding with an ample supply of *Picea* and *Abies* seed. The youngest stages of tree growth appear to be the most critical in these dry areas. Once individuals have passed a certain critical size they appear more resistant to drought (perhaps because root systems are sufficiently well developed). The occurrence of a few tree-size *Picea glauca/engelmannii* in and near stands 24-J-I and 55-J-I supports this hypothesis. "Unusual" conditions may thus permit the establishment of the climax species.

The distributions of all tree species in each of the five Intensive Stands were found to be contagious when sampled with 5 x 5 m quadrats (see p.102 to 111). Since the size of quadrats used in sampling restricts the

size of clumps which can be detected (see Greig-Smith p. 56, 1964) the analysis of quadrat data to determine patterning of trees is valid only for clumps which occupy areas of about 25 m². But because the quadrats used in the analysis for pattern were contiguous, the density per quadrat could be mapped and larger scale patterns seen. For example, in stand 24-J-I the map of pine density (Fig. 202) shows the very distinct areas of high and low density, and in stands 26-J-I, 41-B-I, and 47-B-I density gradients can be seen.

Greig-Smith (1964) emphasizes that the detection of non-randomness is "not an end in itself" (p. 56) but rather it is a first step in the determination of causes of plant distributions. Therefore, having illustrated the presence of contagious tree distributions, it was ecologically imperative to search for causal factors. In the case of stand 24-J-I, the patterning of trees was found to be closely correlated with differences in soil texture which were hypothesized to be important in affecting the total amount of water available to trees as well as affecting the ease with which they can become rooted. Thus the trees are more dense on the "dunes" and less dense on the gravelly soil.

Because of the dominant influence of trees in the creation of microhabitats within the community, the contagious distribution patterns detected in the understory plants in stand 24-J-I can be explained in part by

reference to the distribution of trees. Similar correlations between tree and understory plant distribution patterns were found in the other four stands. Of course, both the trees and understory species might be responding to a common external factor such as availability of water or soil nutrients. Much more intensive environmental and autecological work will be required to show the degree to which both trees and understory may be responding to common environmental factors as well as to the extent that the species patterns are biologically interdependent.

As stated earlier, the detection of non-randomness is a starting point for much ecological work. Thus it is important that the type and scale of patterning be accurately determined and this means that adequate tests must be performed. Where doubt exists as to the meaning of the results of a test, then more tests must be done. Stand 26-J-I is a case in point. The distribution of pine trees in this stand was found to be adequately represented by the Poisson distribution (see p. 102) thus indicating a possible random distribution. But because a density gradient may also fit a Poisson distribution, it was possible to test the geographic homogeneity of the pine and prove that the pine was not randomly distributed. The density gradient (*i.e.* contagious distribution) of pine might have gone undetected had the stand not been sampled by using a block of 400 contiguous quadrats which permitted a geographic test of homogeneity to be performed.

On the basis of the "Gaussian Principle" (Odum 1959), it is obvious that the plant species occupying a single stand must be occupying different niches within the area. The species distribution data from the 400 contiguous quadrats in each Intensive Stand have given some insight into the optimal habitats of certain species relative to other species. "Relative optimal habitats" are emphasized because in these stands the potential habitats of species overlap one another, and thus niche partition or habitat "compression" (MacArthur and Wilson 1967) occurs.

Two species with high stand presence (from Primary Survey) and therefore similarly wide ranges of habitat are *Arctostaphylos uva-ursi* and *Linnaea borealis*. *Arctostaphylos* typically occupies xeric habitats such as open pine woods, whereas *Linnaea* is more typical of cool, shaded forests. When these two species occur together in one stand, they are not randomly associated. In stand 24-J-I, it is clearly seen that *Arctostaphylos* is more abundant around the edges of the more shaded (and presumably cooler and moister) dense areas of pine. Thus within stands, it can be seen that there is partitioning of microhabitats between species such that distribution patterns of presence and abundance are not random even in what at first may appear to be uniform habitats.

Linnaea, however, does not always occupy the moister sites in pine forests. In stand 47-B-I of the Moist Forest Class for example, is more abundant in microhabitats

which would be described as "drier" relative to others within the stand (see p. 143); species such as *Ledum*, *Arnica*, *Equisetum* etc. reach their greatest abundance in the "moister" areas of this stand.

In order to prove the presumed moisture differences between points in one stand as just described, more intensive study is required. But if the species patterns described are actually being controlled by environmental factors and not chance, then these patterns may be used as indicators of microhabitat differences within stands.

The hummocks in stand 55-J-I (described on p. 97) are notable because they are not common in the pine forests studied. It is interesting though, that the species patterning is not well correlated with positions on the hummocks as is the case on hummocks in *Picea mariana*-*Sphagnum* communities (personal communication, Mr. T. Laidlaw, Department of Botany, University of Alberta). There is a correlation between the NE corner of the stand which has hummocks and the distribution of certain species (see p. 183); this corner is lower and moister than the rest of the stand. It is not certain whether there is any cause-effect relationship between the moister habitat and the presence of hummocks.

Lutz (1940), and Lyford and MacLean (1966) have reported detailed studies of hummocks in forested areas of eastern North America. Lutz describes the mixing of the surface caused by the uprooting of trees as a form of

natural cultivation. Lyford and MacLean discuss the differential occurrence of several tree species on the tops of hummocks as compared with the depressions between hummocks. Field notes I made in stand 55-J-I make repeated reference to the occurrence of pines on the tops of hummocks. This may be due to lower seedling mortality on fine soil as compared with very gravelly soils (see also discussion of tree distribution in 24-J-I p. 201). Some hummocks contain charcoal. Thus it appears that these mounds were created by soil which was uplifted by tree roots when the trees fell after being killed by fire. Because the pines are smaller and very shallow rooting in this area, depressions resulting from the removal of the soil when trees are uprooted are quite small compared to those which Lyford and MacLean describe.

Attributes of the pine population which have proved to be very useful are the frequency distributions of diameter size-classes, age-structure, and basal area. Basal area was shown by Smithers (1961) to be well correlated with physiographic site quality and stand age up to 60 years. He found basal area to be relatively unaffected by tree densities greater than 230 stems per acre (*ca.* 570 stems per H). Data from this thesis (Table 4) have also shown that basal area does not correlate well with other attributes of the tree population such as mean tree height, density, or DBH. There is a weak negative correlation between basal areas and mean crown depth and a

weak positive correlation between basal area and elevation. Basal area may therefore serve as an indicator of the productivity of particular sites and thus act as a basis for comparing sites.

The age-structure of the species of the tree stratum together with the frequency distribution of diameter size-classes has revealed much information about the historical development of each individual stand. Where a wide range of diameters and ages exists, and no burn scars are present, it is evident that establishment of the present forest was relatively slow. On the other hand, a narrow range of ages and diameters indicates very rapid establishment of the present stand. If frequencies of both diameters and ages are known for ALL sizes of individuals of a species, then much information about the past history of a stand could be determined. Predictions about future development of the stand could be made if a "Life Table" (Deevey 1947) of the tree species was known. In this thesis, life table statistics for five stands were determined in part and proved invaluable in describing the historical development of these sites. Information was lacking, though, concerning both the ages of individuals in the smallest size-classes and mortality rates in all classes. Some information about the latter was available from the density of dead individuals.

A section entitled the "Vegetational Comparison and Contrast of Intensive Stands" was presented earlier (p.114

Caution must be exercised for the following reasons when trying to relate that section to the description of Forest Types:

1. the Forest Types are abstract, synthetic units the attributes of which may or may not all be present in any particular example of the Type; and conversely, any stand which is classed as a member of a Type may show varying degrees of the characteristics of the Type;
2. It is an unsound procedure to try and strengthen the concept of the Forest Types by extrapolating characteristics found in the specific, isolated examples of the types (*i.e.* the Intensive Stands).

The comparison of the five Intensive Stands, therefore, should not place too much emphasis upon the floristic similarities and dissimilarities between the sites. Much information was gained, however, when the five sites were studied in detail; for example, (1) the niche relationships and spatial distribution patterns of many species were discovered; (2) the population dynamics, successional status, and past history of the sites was determined; and (3) an insight into the complexity of the edaphic-factor-complex was obtained.

The study of available soil nutrients in five pine forests of Banff and Jasper revealed (1) that soil nutrients are not evenly distributed within a stand and (2) that there are directional changes in the quantity of

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nutrients present in the soil through the growing season. The uneven distribution of nutrients within a stand can result from either or both of the following: (1) distributions of parent materials are not uniform; and (2) plants tend to concentrate nutrients in their tissues to a level specific for each species and regardless of the habitat in which the plants grow (Gagnon *et al.* 1958). Thus regarding (2), as plants or their parts die and are decomposed, small localized patches with higher than average nutrient content are formed.

The direction of change of nutrient availability through the growing season is related to the relative rates of uptake and release of nutrients. During June and July when temperatures and moisture are both sufficiently high, plant growth and decomposition, and parent material weathering are maximal. During August the rate of these processes decreases. From this study it appears that during June and July nutrient uptake dominates these three processes such that total nutrients available in the soil decreases. During the latter part of the growing season, however, plant growth has diminished to the point where nutrient build up from weathering of parent materials and decomposition of organic matter become dominant processes.

In searching for correlation between variability in edaphic factors and variability in vegetation, only Pearson's Product Moment correlation "r" was calculated.

This method tests only for linear correlations. Because low "r" values were found does not necessarily mean that no correlation exists, for non-linear correlations, *e.g.* parabolic correlations could be present. However, visual examination of computer plotted scatter diagrams of the relationships between variables did not reveal any obvious non-linear relationships.

Precipitation records for the Intensive Stands during the summer of 1968 indicated the importance of local storm patterns in determining the amount of precipitation received by any particular site. It is suggested, although further proof is required, that certain areas of the Parks consistently receive rain from local storms whereas other areas only rarely receive significant amounts of such precipitation.

Man's influence upon the pine forests of Banff and Jasper varies from nil to extensive. The majority of the forests at higher elevations have not been disturbed primarily because of poor access (access roads to new ski areas and sky-line roads may change this). On the other hand, low elevation forests have and still continue to be used in a variety of ways. Up until a few years ago, logging operations were active in the Spray River Valley in Banff and the Whirlpool River Valley in Jasper. Fortunately precipitation is good in these areas and forests are slowly regenerating.

The recent great demand for increased camping

facilities has seen the development and extension of large campgrounds primarily into the pine forests in the valley bottoms (eg. Whistlers, Wapiti, and Wabasso in Jasper and Tunnel Mtn., Lake Louise, and Protection Mtn. in Banff). The immediate and most obvious effect of large numbers of people walking through a relatively confined area of forest is the destruction of the understory through trampling. This is particularly so in the drier sites where the vegetation dries out during periods of the summer and is very susceptible to trampling damage (this is especially true of terrestrial lichens).

Perhaps the greatest destruction of forests in the two Parks at present (excluding possible fires) is the method of road building. The cutting of wide swaths for super highways with lovely broad stretches of planted grass seem unnecessarily wasteful of large areas of forest. It is true that good highways permit more people to see more of the Parks but I feel that recent highway construction has been excessively damaging to the natural beauty of the mountain areas. It must be remembered that we are committed to the protection of these mountain Parks for all future generations and not their development at the expense of destroying any of their natural features.

XIV. *PINUS CONTORTA* VEGETATION OF REGIONS ADJOINING
BANFF AND JASPER

Cormack (1953) described two types of coniferous forest succession in the Alberta foothills: (I) "pine and spruce to spruce climax", and (II) "pine to spruce climax". Many of the forest sites I studied in Banff and Jasper Parks were similar to the first and especially the second stages in each of the two four-stage sequences that Cormack described, although certain differences were also evident. The feather moss stands 9-B and 26-J were similar to "stage 2" of the "pine and spruce to spruce climax" series. The conspicuous, pale, yellow-green, feather moss carpet, the abundance of *Peltigera* spp. and the sparse flowering plant flora of which *Linnaea borealis*, *Cornus canadensis*, *Pyrola secunda*, *Pyrola virens*, *Ledum groenlandicum*, and *Shepherdia canadensis* are the most abundant, all indicate the floristic and perhaps ecological affinities between these forest sites.

The majority of those stands in Banff and Jasper located in the valley bottoms and on the lower valley walls and ridges resemble "stage 2" of the "pine to spruce climax" sequence. The thin moss carpet composed of several species, the abundance of *Cladonia* spp., the well developed dwarf shrub stratum, and the scattered occurrence of *Shepherdia canadensis*, *Rosa* spp. and *Ledum groenlandicum* relate Cormack's forests to the *Shepherdia* type described for Banff and Jasper. Cormack noted the nearly continuous

dwarf shrub stratum as a characteristic feature of this stage. Although he states that high tree densities reduce the density of the understory plants, this in itself would not account for the incomplete development of a dwarf shrub stratum in many of the Banff and Jasper stands which otherwise are of the "Trend II, stage 2" type. It may be that some of the Banff and Jasper stands have less available moisture than the "Trend II" type. A decrease in available water could be partially responsible for the reduction in plant population sizes.

Illingworth (Illingworth and Arlidge 1960) has classified *Pinus contorta* forests of the south central interior of British Columbia according to a "forest site type" classification similar to that developed by Cajander (1926). The five major site types Illingworth described are:

1. *Cornus canadensis* - Moss site type,
2. *Calamagrostis rubescens* site type,
3. *Calamagrostis rubescens* - *Vaccinium scoparium* site type,
4. *Calamagrostis rubescens* - *Arctostaphylos uva-ursi* site type,
5. *Arctostaphylos uva-ursi* - Lichen site type.

These forest site types are similar in physiognomy and with certain exceptions, in species composition to the Banff and Jasper sites described in this thesis. Major species present in B. C. but not in Banff and Jasper are: *Pachystima myrsinites*, *Lupinus* spp., *Clintonia uniflora*,

Solidago spathulata, *Mahonia aquifolium*, *Tiarella unifoliata*, and *Lilium parviflorum*.

The "Cornus - Moss Site Type" is similar to stands 19-J, 26-J, 28-J, 29-J, and 38-J in that they occur in moist areas of the subalpine forest and have a developing understory of *Picea engelmannii* and/or *mariana*. The high shrub stratum is similar in that *Alnus* (*A. crispa* in Banff and Jasper in place of *A. tenuifolia*) and *Shepherdia canadensis* are present. *Pachystima* does not occur in the Banff and Jasper stands but *Vaccinium scoparium* does. The two regions have the same characteristic abundance of *Cornus canadensis*, and *Chimaphila umbellata*, *Pyrola secunda*, *Arnica cordifolia*, *Aquilegia formosa*, *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis* are also in common. The scarcity of ground lichens in this forest type was characteristic of some of the Banff and Jasper stands such as 19-J, 28-J, and 38-B.

The "Calamagrostis Site Type" is not well represented in Banff and Jasper. If *Elymus innovatus* takes the place of *Calamagrostis rubescens* on drier sites then stands such as 54-J and 4-B may resemble this type. Shrub development is not good but *Shepherdia canadensis*, *Spiraea lucida*, *Rosa* spp. and *Vaccinium caespitosum* are to be found in both regions. The presence of a few plants of *Thalictrum* spp. and *Antennaria racemosa* with only a small amount of *Arctostaphylos uva-ursi* tends to support the similarity of these areas. A general abundance of mosses (including

feather mosses) is also a common feature.

The "*Calamagrostis-Vaccinium scoparium* Site Type" does not appear to be clearly represented in the Banff or Jasper stands. Stands 16-J, 17-J, and 37-J might, except for the paucity of *Vaccinium scoparium* and *Elymus innovatus*, be associated with type because of their poorly developed understory. Illingworth describes his "*Calamagrostis-Arctostaphylos*" type as part of a continuum of variation between the *Calamagrostis* and the *Arctostaphylos* - lichen types. The position of a stand along this gradient appears related to the availability of soil water. Stands 32-J, 24-J, 35-J, and 38-B resemble the latter type. The sparse high-shrub stratum primarily of *Rosa acicularis* and *Shepherdia canadensis* and the dwarf shrub stratum with *Vaccinium* sp. and *Arctostaphylos uva-ursi* plus *Linnaea borealis* all indicate the phytoecological affinities between the B. C. and the Banff and Jasper sites. *Peltigera* spp. and *Cladonia* spp. were widespread but not as abundant as Illingworth described for B. C.

The "*Arctostaphylos* - Lichen type" occurs on xeric woodland sites in interior B. C. None of the Banff or Jasper stands appear as xerophytic or open as this type, but the open areas of stand 24-J approach it.

In comparing Illingworth's description of lodgepole pine communities in B. C. with those for Banff and Jasper, a few major contrasts are apparent:

1. climax tree species were well established even on the driest pine sites reported in B. C., but little or no such establishment was found in the

driest pine sites in Banff and Jasper.

2. A type of limited occurrence in B. C.--the *Vaccinium scoparium* type was described as being the southern counterpart of the *Arctostaphylos* - Lichen type i.e. occurring on "dry, rocky or gravelly soils". In Banff and Jasper, the *Vaccinium scoparium* type forest occurs on moist to mesic, not xeric sites.

The "*Equisetum* - *Sphagnum* Site Type" which occurs around marshes and lakes in B. C. also occurs in Banff and Jasper but it was not studied in this investigation. The "*Pachystima*" and "*Heracleum lanatum*" site types were not studied in Banff or Jasper. However, Dr. G. H. La Roi (Department of Botany, University of Alberta) reports finding abundant *Heracleum lanatum* with *Pinus contorta* on eutrophic, wet SW slopes of Signal Mtn., Jasper (personal communication).

Thus, with slight adjustments for understory species differences, there appears to be a large degree of similarity between *Pinus contorta* forests in Banff and Jasper and those of the south central interior of B. C.

Moss (1953) classified the pine (*Pinus banksiana* and *P. contorta* var. *latifolia*) vegetation of northwest Alberta into two "faciations": (1) the "pine - feather moss faciation" characterized by *Hylocomium splendens*, *Pleurozium schreberi*, *Linnaea borealis*, *Pyrola* spp., and *Cornus canadensis*, and (2) the "pine - heath faciation"

characterized by *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea*, *Elymus innovatus*, *Oryzopsis pungens*, *Polytrichum* spp. and *Cladonia* spp. Although complete species lists were not given for each 'faciation' or consociation, it is apparent that Moss' "pine - feather moss faciation" is similar both physiognomically and to a certain degree floristically to the feather moss type which I have described in earlier sections. There is a similar correspondence between his "pine - heath faciation" and the *Arctostaphylos* and *Elymus* types in Banff and Jasper. There appears to be an ecological equivalence between these similar forests in the two regions. Specifically, succession to a spruce-fir climax is quite evident in the more moist feather moss type forests; whereas, on drier sites where *Arctostaphylos* and *Elymus* are abundant, succession to spruce-fir is greatly retarded if at all evident.

Moss described *Alnus crispa*, *Rosa* spp. *Salix* spp. and *Maianthemum canadense* as being common in both "faciations". The latter species was not found in the Banff or Jasper pine forests. *Salix* spp. and *Rosa* sp. were never abundant in Banff or Jasper but were constantly present. *Alnus crispa* on the other hand, was a characteristic species of certain cool, moist forests in the Parks and either completely absent or rare in the other forests--it was not common on the dry sites as Moss described for NW Alberta.

Horton (1956) has made an extensive study of the "Ecology of Lodgepole Pine in Alberta". The present study

is in agreement with many of the conclusions presented by Horton. In particular there is agreement on (1) the importance of fire to the present abundance of *Pinus contorta*, (2) the general concept that the pine is seral to spruce-fir, (3) the effect of stand history upon vegetative patterns, and (4) stand structure and stocking following fire.

There are details in Horton's work with which I disagree. Horton did not give precise locations of the areas he sampled, but from the map presented, his stands in Banff and Jasper all appear to be in the cool, moist and mostly higher elevation subalpine areas. No areas appear to be sampled in the lower portions of the Athabasca and Bow Valleys within the Parks. These low valley areas bear strong phytoecological similarities to the high foothills and montane phytogeographical divisions rather than the subalpine division. (Horton recognizes four forest divisions in Alberta:

1. Montane Division--SW corner of Alberta
2. Subalpine Division--Mountain region
3. High Foothills Division--transitional between #2 and #4
4. Low Foothills Division--mixedwood region between foothills and boreal regions.)

Exception is taken to Horton's conclusion that because the pine vegetation is explicable in terms of the vegetational continuum concept, that classification of different sites based upon the understory vegetation would be

"pointless". As he says, numerous combinations of understory species occur, but because the understory of pine forests is often floristically simple and dominated by a great abundance of one or two species it is possible to classify different types of pine forest at least within one phytogeographical region. Such a classification does not necessarily refute the continuum nature of the vegetation. Rather it helps to clarify the relationships between the various parts of the continuum. Furthermore, the classification is ecologically significant in that the understory vegetation may be more sensitive to habitat changes, particularly those relating to available water, than is immediately apparent from the pine.

Horton has de-emphasized the distinctness of the xerophytic pine forests which Moss (1953) called the "pine-heath faciation", Cormack referred to as "stage 2" of the "pine to spruce climax", and what I have called the *Arctostaphylos* type. Horton indicated *Arctostaphylos uva-ursi* to be equally abundant in all four of the Forest Division he recognized in Alberta. Such was not the case for the moist and xeric sites in Banff and Jasper Parks. In his "general lodgepole pine association" for Alberta: "*Pinus* - *Picea* - *Vaccinium* - *Elymus* - *Linnaea* - Feather moss - *Peltigera*" he does not mention *Arctostaphylos*, and *Elymus* and *Linnaea* are the only indications that this heterogeneous "association" may have included the most xeric sites.

Arctostaphylos tends to be most abundant in open,

dry forests which often resemble a climax community in that the pine reproduces as the tree canopy opens due to the falling of old trees. Spruce and fir are not aggressive, *i.e.* do not show definite signs of reproducing in some of these areas despite the often readily available seed sources. Horton, in his discussion of succession, has apparently used only the availability of spruce and fir seed--not actual reproduction--as sufficient evidence to conclude that these areas would all eventually become spruce-fir forests. Information obtained during the present study does not agree with this generalization. There were sites where pine was reproducing but spruce and fir were not, despite the availability of seed for spruce-fir establishment.

Thus my own findings agree with those of Horton in many respects but also differ with his on certain aspects of classification and succession.

The literature concerning *Pinus contorta* to the south of Banff and Jasper which was available to me, primarily refers to the different kinds of forest tree species and their distributions with only bare mention of associated understory plants. Cary (1911) for example, describes lodgepole pine in Colorado as occurring on sites which are cooler and moister than those occupied by *Pinus ponderosa* but which are warmer and drier than those occupied by *Picea engelmannii* and *Abies lasiocarpa*. He described *Populus tremuloides* as a common associate of lodgepole pine.

Larsen (1930), working in the Rocky Mountains of

Montana, similarly describes lodgepole pine as occurring above the zone of *Pinus ponderosa* and below the zone of *Pinus flexilis*, *Abies lasiocarpa*, and *Picea engelmannii*. He found lodgepole pine often associated with *Pseudotsuga menziesii*, but that the pine grew better on cooler and moister sites, whereas, the *Pseudotsuga* grew better on warmer and drier sites. A similar condition exists in Banff and Jasper where *Pseudotsuga* dominates the xeric south and west slopes of ridges in the valley bottoms while *Pinus contorta* dominates the more mesic sites between and on north and east slopes of the ridges.

Comparisons of forest types between Banff and Jasper, and areas to the south has not been easy because of the lack of vegetation data available to me regarding the *Pinus contorta* vegetation to the south. *Pinus contorta* appears to occupy as wide a range of habitats to the south as it does in Banff and Jasper. It is most abundant where fires are prevalent. It can occur as forests of pure pine or as a mixed coniferous and deciduous forest. D. T. Mason (1915) describes Feather Moss type pine forests in Montana while Larsen (1930) also describes presumably drier types of pine forests where *Festuca ovina* and *Cercocarpus ledifolius* occur as understory plants.

Klyver (1931) describes two types of pine forest amongst the major plant communities of the Californian Sierra Nevada Mountains. (1) The "Fir-Lodgepole Forest" occurs extensively in the areas between 7,000 and

10,500 ft. *Pinus contorta* is co-dominant with *Abies magnifica* in a climax forest on cool "wet" sites at higher elevations, and co-dominant with *Abies concolor* at lower elevations. A variety of Forest Types occur as would be expected considering the 3,000 ft elevational range alone.

(2) The "Lodgepole Forest" consists of pure stands of *Pinus contorta* throughout the region studied by Klyver. It occurs on mesic to dry mesic sites. *Juniperus occidentalis*, *Artemisia tridentata*, and *Cercocarpus ledifolius* dominate the understory on many sites.

For the most part, the understory appears dominated by plants of southern distribution but a few boreal species are present: *Pyrola secunda*, *Corallorhiza maculata*, *Habenaria unalascensis*. Klyver's brief description, in addition to the major floristic differences make it difficult to cite ecological similarities between the Sierra Nevada and Banff and Jasper except to say that *Pinus contorta* occupies mesic forested sites in both areas, i.e. there is a zone of more xerophytic forest below the *Pinus contorta* in both regions. To the south *Pinus ponderosa* forms the drier forest and in the Parks *Pseudotsuga* grows in the drier sites. In contrast to Banff, Jasper, Montana, and Colorado, where *Pinus contorta* is succeeded by a *Picea-Abies* forest at higher elevations, the Sierran *Pinus contorta-Abies* forest is a stable climax community right to tree line.

Raup (1934) reported for the Peace and Upper Liard

River regions of Canada, that *Pinus contorta* occurred on uplands (ca. 1,600 ft) generally above a zone of *Pinus banksiana*. He describes two types of pine forests:

(1) "very dry pine woods" with *Shepherdia canadensis*, *Arctostaphylos uva-ursi*, *Elymus innovatus*, and *Peltigera aphthosa* being dominant species, and (2) "rich pine woods" with *Alnus crispa* and *Vaccinium vitis-idaea*. The former of these two types appears similar to the *Arctostaphylos* and *Elymus* types of Banff and Jasper while Raup's latter types may correspond to the *Alnus crispa* type of the two Parks. Raup's listing of *Peltigera aphthosa* as a dominant member of the dry pine forests is not supported by the present study in which it was found only in moist places.

The seral nature of *Pinus contorta* forest was emphasized by Raup and Denny (1950) when they hypothesized that the forests of the south part of the Alaska Highway would become composed of *Picea glauca* with the exception of wet areas where *Picea mariana* would dominate, and of very dry areas where *Pinus contorta* "might maintain an open forest". The pyric-physiographic climax (Oosting 1956) of pine on very dry sites such as the drier *Arctostaphylos* and *Shepherdia* type forests found in Banff and Jasper may be part of a more general phenomenon as postulated in the work of Moss (1953) and Raup and Denny (1950).

Jeffrey (1964) has reported on six types of *Pinus*

1. The first part of the document is a letter from the President of the United States to the Congress.

2. The second part is a report from the Secretary of the Treasury on the state of the Union.

3. The third part is a report from the Secretary of the Navy on the state of the Navy.

4. The fourth part is a report from the Secretary of the War on the state of the War.

5. The fifth part is a report from the Secretary of the Interior on the state of the Interior.

6. The sixth part is a report from the Secretary of the Agriculture on the state of the Agriculture.

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15. The fifteenth part is a report from the Secretary of the Navy on the state of the Navy.

16. The sixteenth part is a report from the Secretary of the Interior on the state of the Interior.

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26. The twenty-sixth part is a report from the Secretary of the Navy on the state of the Navy.

27. The twenty-seventh part is a report from the Secretary of the Interior on the state of the Interior.

28. The twenty-eighth part is a report from the Secretary of the Agriculture on the state of the Agriculture.

contorta forest along the Lower Liard River of the North West Territories. In this area the species is confined to uplands between 1,800 ft and 3,800 ft (timber line). The five types are as follows:

1. "timber line forest" 3,800 ft
Pinus contorta plus *Picea glauca*, *P. mariana*,
Abies lasiocarpa, and *Larix laricina*.
2. "Lodgepole pine--west slope forest" 3,500 - 3,700 ft
Pinus contorta with an understory of *Picea mariana*, and *Abies lasiocarpa*.
3. "Mixed coniferous forest--high elevation" 2,300 - 2,600 ft
Pinus contorta and *Picea glauca*, plus *Picea mariana*, and *Abies lasiocarpa*.
4. "Mixed coniferous forest--low elevation", 1,800 - 2,300 ft similar to #3 but *Populus tremuloides* replaces *Abies lasiocarpa*.
5. "Lodgepole pine--lichen woodland" 1,800 - 2,300 ft, an open forest of *Pinus contorta*, *Picea glauca*, *Populus tremuloides*, and *Betula papyrifera*.
6. "Dry Rocky Slope forest"
Pinus contorta and *Picea glauca* with an understory of *Juniperus horizontalis*.

As can be seen from the above, no "pure" *Pinus contorta* forests were described although this species formed the dominant tree of some types such as #2, 5, and 6. Jeffrey has described the most common forest types he found

and has emphasized the seral nature of the pine community.

The "mixed coniferous forests" (high and low elevation types--#3 and #4) are somewhat similar to the Feather Moss type forests of Banff and Jasper. Jeffrey's "dry rocky slope forest" (type 6) may be floristically similar to the *Arctostaphylos* type of the Parks. Since more detailed information about the physiognomy and floristics of these Liard River forests is not available, a more thorough ecological comparison cannot be made at present.

XV. SUMMARY

1. The objectives of the study were to describe and classify the *Pinus contorta* vegetation of Banff and Jasper and to relate variability in the vegetation to selected factors of the physical environment. The historical development and successional status of the pine stands were also investigated.
2. A total of 63 major stands (30 in Banff and 33 in Jasper) and 15 minor stands (13 in Banff and 2 in Jasper) were located by use of aerial photographs (1949-1951) and direct field observations. The major sites had to meet the following criteria before being studied:
 - (a) greater than 75% of the basal area of the tree stratum had to be pine;
 - (b) the stand had to be greater than about 16 hectares;
 - (c) topography was to be relatively uniform;
 - (d) human disturbance was to be minimal.
3. The field work consisted of two major phases:
 - (a) Primary Survey (1966) of the pine vegetation in both Parks, and
 - (b) Intensive Study (1967 and 1968) of five stands which were selected as being representative of different types of pine dominated communities.
4. The Primary Survey made use of a plotless technique of sampling. Information regarding the following

were obtained: tree basal areas by species (both living and dead); pine tree density; tree diameter size-class distribution; depths of the photosynthetic crowns of trees; tree height; tree ages by diameter size-classes; cover, vitality, and phenological condition of all vascular plant species present; the presence of non-vascular plants; the slope, aspect, elevation, and soil of each stand.

5. Having completed the Primary Survey, the following tentative classification of forest types was constructed based upon both floristic and physiognomic criteria:

- (a) stands with a conspicuous high shrub stratum
 - (i) predominant shrub *Menziesia glabella* (47-B-I)
 - (ii) predominant shrub *Shepherdia canadensis* (55-J-I)
 - (iii) predominant shrub *Alnus crispa*
- (b) stands lacking a high shrub stratum but with a conspicuous low or dwarf shrub stratum
 - (i) *Vaccinium scoparium* dominant (47-B-I)
 - (ii) *Arctostaphylos uva-ursi* dominant (24-J-I)
- (c) stands lacking a conspicuous high, low, or dwarf shrub stratum
 - (i) *Elymus innovatus* abundant
 - (ii) Feather mosses abundant (26-J-I)

6. Five stands from the Primary Survey were selected for intensive study (indicated in (5) above by

stand numbers). The sampling procedure involved the laying out of 400 5 x 5 m contiguous quadrats so as to cover a square area of one hectare. The following information was obtained from each of the quadrats:

- density of tree species by size-classes from seedlings to trees (trees were divided into three-inch diameter classes)
- the presence and cover of all vascular, and dominant non-vascular plants;
- the degree of exposure of the quadrat corners to the sky;
- point cover of tree stratum at quadrat corners;
- the temperature of the soil at 20 cm at each quadrat corner.

A soil sample was collected and profile described from a pit (75 cm deep) dug in a randomly selected quadrat.

7. The microtopography of each of the five sites was mapped (contour interval = 10 cm).
8. Information regarding both the tree densities per quadrat and the cover abundance of understory plants permitted the mapping of species distribution patterns. By comparing the maps of species within one stand to each other and to the topographic map, the inter-relationships between species distributions and microtopography became quite clear for

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many, but not all species.

9. Twenty-five quadrats selected in a restricted random manner were studied in greater detail to determine the age and size structure of the tree stratum as well as its basal area. Also, a quantitative estimate of the cover of the major species present in each stand was obtained by means of a point sampling technique.
10. Precipitation was measured at each Intensive Stand during the 1968 growing season. In Jasper, stand 55-J-I received more rain during both sampling periods than did Jasper townsite. Stand 26-J-I received slightly less rain during the spring but more during the late summer than did Jasper townsite. Stand 24-J-I received the least precipitation of any site during the first part of the growing season and it received slightly more rain than the townsite in the latter part of the season. In Banff, the two stands received considerably more rain in the first part of the season than did the Banff townsite, indicating the effect of local storm patterns in the early part of the season.
11. At the beginning of June, August, and September (1968) soil samples were collected from the five Intensive Stands. A nutrient analysis of the samples revealed directional variability through the growing season as well as variation between

sampling points in the degree of fluctuation within each stand. Nutrient uptake and release occur simultaneously but during the early part of the growing season, uptake appears to be the dominant process while release or build up dominate during the latter part of the season.

12. The floristic/physiognomic classification proposed for the pine vegetation was substantially corroborated by means of a Cluster Analysis. Three main classes of pine vegetation were evident in the analysis: Moist, Mesophytic, and Xerophytic Classes.
13. The Moist Class was composed of four forest types:
 - (a) *Menziesia*, (b) *Alnus*, (c) Feather Moss, and
 - (d) *Vaccinium scoparium*. The first type was a well-defined unit. The second and third types had central "cores" of very similar stands but also had subsidiary or transitional stands associated with them. The last type had a moist and a mesic phase, the former at higher elevations than the latter.
14. The Mesophytic Class was composed of three forest types: (a) *Shepherdia*, (b) *Elymus*, and (c) Mesic High Subalpine. The latter represents two groups of stands in which species populations are unusually small. The *Shepherdia* type has a moist Banff

- phase and a more dry Jasper phase. The *Elymus* type appears to be transitional on a moisture gradient between the Mesic and Xeric Classes.
15. The Xerophytic Class was composed of the *Arctostaphylos* type only, except that a pine savanna found in Jasper may also belong in this Class, but it was not studied.
 16. The three Classes may be ranked according to elevation: Moist--high elevation, Mesic--mid elevation, and Xeric--low elevation. Exceptions occur especially in the Moist Class where both climate and topography combine to produce moist habitats at low elevations.
 17. The *Menziesia* type is found in cool moist sites at higher elevations. *Rhododendron albiflorum*, and *Phyllodoce* spp. are both characteristic of high elevations. Pine growth appears good in these sites but succession to *Picea-Abies* appears to be quite rapid.
 18. The *Alnus* type is common at mid-elevations on eutrophic, cool, moist sites. The type grades into the *Vaccinium scoparium* and Feather moss types. Succession to *Picea-Abies* forests appears rapid.
 19. The Feather Moss type is ubiquitous in that it occurs over a wide range of elevations. All stands of this type have closed tree canopies and occupy moist sites. Succession to *Picea-Abies* is good

- on most sites but not all.
20. The *Vaccinium scoparium* type is best developed at high elevations usually above the zone of *Menziesia*. Abundant *Vaccinium scoparium* does occur on cool moist sites at mid-elevations and also on mesic sites at lower elevations. Succession to *Picea-Abies* is rapid on the moist sites but slower on the mesic sites.
 21. The Mesophytic High Subalpine type (5,400-6,100 ft) is related to the Feather Moss forest type but the former have much smaller populations of all understory plant species including mosses and thus are recognized as a separate group. Two geographic groups are represented in this type--those on the SW slope of Endless Chain Ridge and those just NW of Maligne Lake. Succession to *Picea-Abies* is neither rapid nor retarded.
 22. The *Shepherdia canadensis* type occurs at mid-elevations (ca 5,000 ft in Banff and 4,000 ft in Jasper). It is represented by a moist phase in Banff and a dry phase in Jasper. The type occurs on warm, mesic sites usually where tree densities are not too high. Succession is not rapid either because of the difficulty experienced by the climax species in becoming established or because of the occurrence of ground fires. *Juniperus communis* is often associated with this type. This type

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- grades into the xerophytic *Arctostaphylos* type.
23. The *Elymus* type occurs at mid-elevations similar to those of the *Shepherdia* type but on drier sites. The *Elymus* type is not common in the two Parks. Succession is slow on these sites.
 24. The *Arctostaphylos uva-ursi* type is predominant in the bottoms of the major valleys where the habitat is warm and dry. It tends to have small species populations of all plants except *Arctostaphylos*. *Elymus* and *Linnaea* may be locally abundant in this type. Succession in this type is often arrested and a type of physiographic pine climax exists.
 25. A residual group of stands which were not classified because of their apparently transitional nature were related to the proposed classification system.

INTENSIVE STANDS

26. The pine trees in the Intensive Stands (excluding 26-J-I) were shown by means of comparison of the actual tree density distributions to the expected Poisson distributions to be non-randomly distributed. The maps of tree density and the variance: mean ratios indicated contagious distributions.
27. The frequency distribution of trees in 26-J-I fits a Poisson distribution but was shown to be non-random by means of a geographic test of homogeneity. From the distribution maps it was

1. The first part of the paper is devoted to a general discussion of the problem.

2. The second part is devoted to a detailed analysis of the various cases which may arise.

3. The third part is devoted to a study of the properties of the various solutions which have been obtained.

4. The fourth part is devoted to a study of the properties of the various solutions which have been obtained.

5. The fifth part is devoted to a study of the properties of the various solutions which have been obtained.

6. The sixth part is devoted to a study of the properties of the various solutions which have been obtained.

7. The seventh part is devoted to a study of the properties of the various solutions which have been obtained.

8. The eighth part is devoted to a study of the properties of the various solutions which have been obtained.

9. The ninth part is devoted to a study of the properties of the various solutions which have been obtained.

10. The tenth part is devoted to a study of the properties of the various solutions which have been obtained.

11. The eleventh part is devoted to a study of the properties of the various solutions which have been obtained.

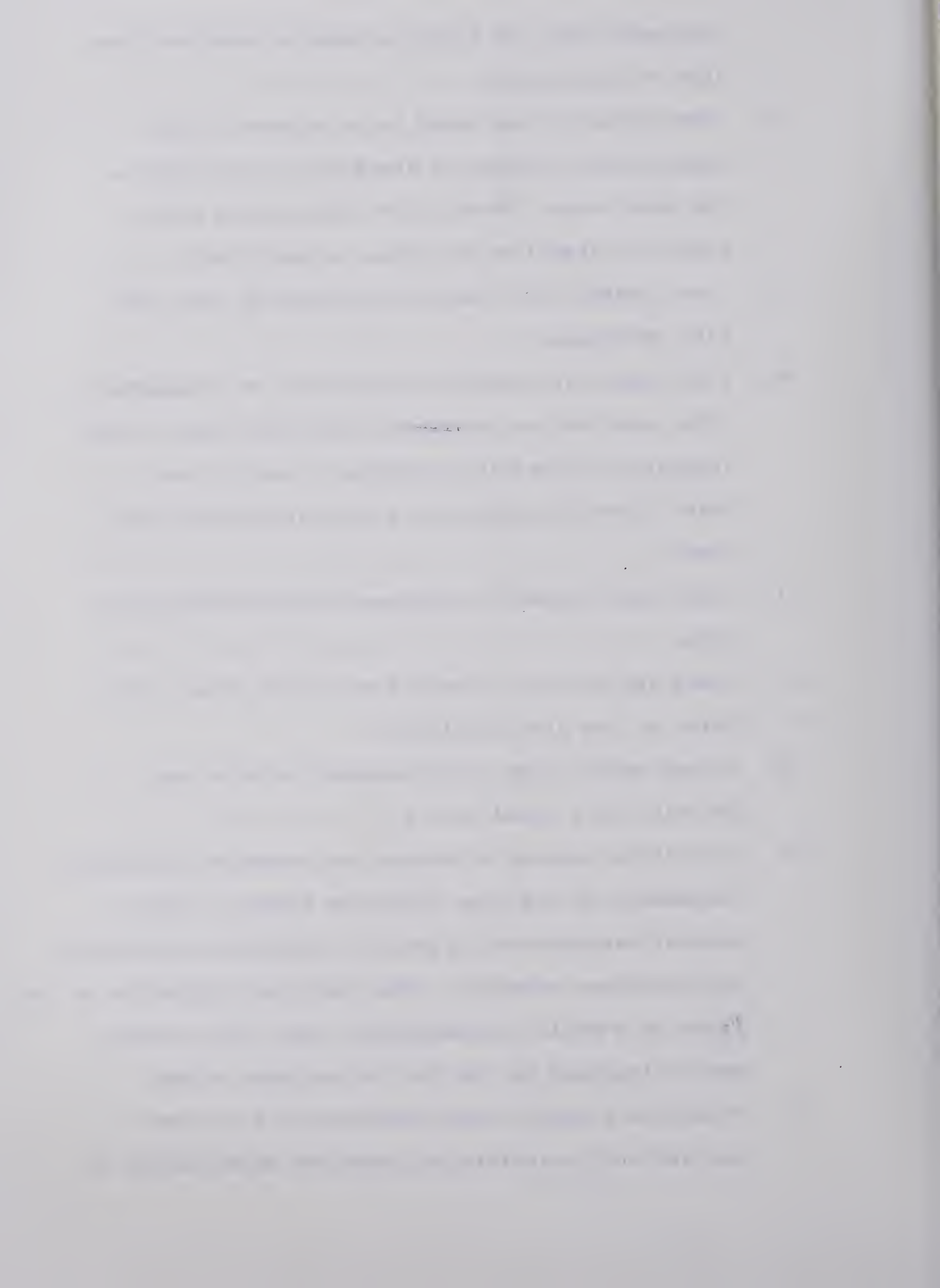
12. The twelfth part is devoted to a study of the properties of the various solutions which have been obtained.

13. The thirteenth part is devoted to a study of the properties of the various solutions which have been obtained.

14. The fourteenth part is devoted to a study of the properties of the various solutions which have been obtained.

15. The fifteenth part is devoted to a study of the properties of the various solutions which have been obtained.

- concluded that the trees followed a gradient from high to low density.
28. Tree mortality was found to be highest in the denser areas of pine in stand 24-J-I and less in the open areas. Stand 47-B-I has greater tree mortality than the less dense stand 41-B-I.
 29. Crown depths were found to increase as tree density decreased.
 30. Tree height was found to be greater on mesophytic sites and less on xerophytic and cool, moist sites (exception--stand 26-J-I which is put in the moist class but occurs in a low, relatively warm area).
 31. Tree cover tended to increase with increasing density.
 32. Stand age did not correlate well with other attributes of the pine population.
 33. A "gap phase" type of replacement of pine was described for stand 26-J-I.
 34. Only three species of shrubs are important structural components of the five Intensive Stands. These species are *Menziesia glabella*, *Shepherdia canadensis*, and *Juniperus communis*. When the pine vegetation of the Parks as a whole is considered, then *Alnus crispa* may be included in the list of dominant shrubs.
 35. *Vaccinium scoparium* and *Arctostaphylos uva-ursi* are the only structurally important dwarf shrubs in



the pine vegetation and feather mosses are the only important bryoids.

36. The density distribution of pine in stand 41-B-I is thought to be a function of distance from seed source and intensity of competition with *Picea* and *Abies*. The distributions of *Picea* and *Abies* in 41-B-I are also shown to be a function of distance from seed source.
37. The distributions of many understory plants in stand 41-B-I correlate with the distribution of trees, eg. *Pleurozium schreberi* and *Cornus canadensis* are more and *Pyrola secunda* is less abundant where *Picea* and *Abies* are more abundant.
38. The contagious distribution of pine in stand 47-B-I appears related to some intrinsic variability in the microhabitats of the site such that certain areas can support greater tree densities than other areas.
39. Although the topography of stand 47-B-I is fairly uniform, microtopographic variation such as shallow depressions or low ridges appear to strongly affect the quantitative distributions of some species. The distribution of the dense deadfall also strongly affects the distribution of understory plants by restricting the potential area which the plants could occupy.
40. In stand 26-J-I, the distribution patterns of

The first part of the paper is devoted to a discussion of the general principles of the theory of the structure of the atom. It is shown that the structure of the atom is determined by the laws of quantum mechanics, and that the laws of quantum mechanics are determined by the laws of the theory of the structure of the atom. This is a circular argument, but it is the only way to proceed.

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both trees and understory plants are strongly affected by the topographic discontinuity between the two adjacent river terraces. The lower terrace is moister (*i.e.* closer to the water table) than the upper terrace. For the understory plants the lower terrace is more shaded than the upper terrace due to the presence of a large population of *Picea mariana* on the former. Species are thus seen to be sorted according to which of these two habitats is more favourable for their growth.

41. Stand 55-J-I represents a physiographic pine climax. Environmental conditions are unfavourable for *Picea* or *Abies* but favourable for *Pinus* to become established and reproduce.
42. As in stand 47-B-I, the understory species in stand 55-J-I are distributed in relation to small differences in microhabitat. Alternating drier and moister zones are evident from the distribution maps of species.
43. The trees in stand 24-J-I occur in clumps of either very high or very low density. The dense areas are associated with raised deposits of silt and sand whereas the more open areas are associated with very gravelly sites. The trees in the dense areas have become established following a fire which did not severely damage trees in the open areas.

44. The distribution of understory plants is closely associated with the distribution of trees in stand 24-J-I. Plants which thrive in more xeric habitats occur either exclusively or more abundantly in the open areas, whereas, plants of mesic habitats are restricted to, or thrive best beneath the denser tree canopy.

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APPENDIX 1

SOIL ANALYSIS: TEXTURE AND AVAILABLE NUTRIENTS

| Plot No. | C | Texture Si | Sa | Pounds N | per P | acre K | Soil re- action (pH) | Conduc- tivity mmhos. | Free Lime CaCO ₃ |
|----------|------|------------|------|----------|-------|--------|----------------------|-----------------------|-----------------------------|
| 1-1-B | 5.5 | 17.3 | 77.3 | 0 | 5 | 102 | 6.8 | .4 | nil |
| 1-1-C | 5.5 | 35.5 | 59.0 | 1 | 0 | 102 | 7.2 | .3 | nil |
| 1-1-D | 6.0 | 12.1 | 81.9 | 0 | 2 | 70 | 7.9 | .3 | nil |
| 2-1-B | 6.1 | 32.6 | 60.1 | 0 | 10 | 226 | 6.2 | .3 | nil |
| 2-1-C | 4.9 | 11.9 | 83.2 | 0 | 2 | 48 | 7.2 | .2 | nil |
| 2-1-D | 6.9 | 7.4 | 85.6 | 0 | 2 | 70 | 7.9 | .3 | 2 |
| 2-1-E | 4.6 | 11.5 | 83.9 | 0 | 0 | 40 | 8.2 | .3 | 5 |
| 2-1-C' | 10.8 | 23.3 | 65.8 | 0 | 0 | 40 | 7.8 | .3 | 5 |
| 2-2-B | 4.5 | 29.2 | 66.3 | 0 | 83 | 183 | 6.8 | .3 | nil |
| 2-2-C | 5.5 | 18.2 | 76.3 | 0 | 26 | 98 | 6.6 | .1 | nil |
| 2-2-D | 4.0 | 13.6 | 82.4 | 0 | 7 | 40 | 7.7 | .2 | 4 |
| 2-2-E | 7.8 | 22.9 | 69.3 | 1 | 0 | 28 | 7.9 | .3 | 5 |
| 2-2-E' | 9.5 | 22.2 | 68.3 | 0 | 2 | 40 | 7.7 | .5 | 5 |
| 2-2-F | 6.1 | 10.0 | 83.9 | 1 | 0 | 40 | 8.6 | .3 | 5 |
| 3-2-B | 5.5 | 15.4 | 79.0 | 0 | 7 | 114 | 6.9 | .2 | nil |
| 3-2-C | 5.0 | 14.2 | 80.8 | 0 | 2 | 52 | 6.4 | .2 | nil |
| 3-2-D | 5.0 | 2.3 | 92.7 | 0 | 2 | 48 | 6.8 | .2 | nil |
| 3-2-E | 5.2 | 0.6 | 94.3 | 1 | 2 | 48 | 7.3 | .1 | nil |
| 3-2-F | 5.2 | 33.6 | 60.8 | 0 | 5 | 110 | 7.7 | .2 | 1 |
| 3-1-B | 6.7 | 37.4 | 55.9 | 0 | 29 | 153 | 6.4 | .3 | nil |
| 3-1-C'' | | | | 0 | 15 | 129 | 6.9 | .2 | nil |
| 3-1-C | 7.5 | 50.7 | 41.8 | 0 | 12 | 222 | 6.7 | .2 | nil |
| 3-1-D | | | | 0 | 15 | 126 | 7.0 | .2 | nil |
| 3-1-E | 6.8 | 36.3 | 56.9 | 1 | 10 | 70 | 7.1 | .2 | nil |
| 3-1-F | 5.3 | 24.4 | 70.3 | 1 | 26 | 86 | 7.2 | .2 | nil |
| 4-1-B | 15.6 | 43.0 | 41.4 | 1 | 43 | 308 | 7.3 | .5 | nil |
| 4-1-C | 15.6 | 35.3 | 49.1 | 1 | 19 | 375 | 6.5 | .4 | nil |
| 4-1-D | 12.4 | 28.8 | 57.8 | 1 | 2 | 133 | 7.7 | .5 | 3 |
| 4-1-E | 21.9 | 27.3 | 50.8 | 1 | 2 | 86 | 7.9 | .4 | 4 |
| 5-1-B | 15.4 | 47.2 | 37.4 | 0 | 7 | 391 | 7.2 | .6 | nil |
| 5-1-C | 14.6 | 46.0 | 39.5 | 1 | 0 | 126 | 7.9 | .5 | 5 |
| 6-1-B | 18.2 | 34.5 | 47.4 | 1 | 2 | 192 | 7.2 | .4 | nil |
| 6-1-C | 25.3 | 27.4 | 47.3 | 1 | 2 | 261 | 7.3 | .5 | nil |
| 6-1-D | 17.1 | 30.1 | 52.7 | 1 | 2 | 137 | 7.8 | .5 | 3 |
| 6-1-E | 26.5 | 26.5 | 47.0 | 0 | 0 | 200 | 8.0 | .5 | 6 |

| Plot No. | C | Texture Si | Sa | Pounds N | per P | acre K | Soil re- action (pH) | Conduc- tivity mmhos. | Free Lime CaCO ₃ |
|----------|------|------------|------|----------|-------|--------|----------------------|-----------------------|-----------------------------|
| 7-1-B | 26.4 | 30.9 | 42.6 | 0 | 5 | 62 | 7.0 | .8 | 1 |
| 7-1-C | 32.6 | 47.7 | 19.7 | 0 | 0 | 66 | 8.1 | .7 | 6 |
| 7-1-D | 16.0 | 55.4 | 12.2 | 0 | 0 | 187 | 8.3 | .5 | 7 |
| 7-2-B | 11.4 | 46.5 | 42.1 | 0 | 12 | 277 | 8.4 | .4 | nil |
| 7-2-C | 13.1 | 37.2 | 49.7 | 0 | 7 | 192 | 7.1 | .3 | nil |
| 7-2-C' | 16.0 | 40.0 | 44.0 | 1 | 2 | 153 | 7.7 | .5 | 1 |
| 8-1-B | 7.5 | 40.9 | 51.6 | 0 | 5 | 126 | 7.1 | .4 | nil |
| 8-1-C | 8.9 | 24.1 | 67.0 | 1 | 2 | 137 | 7.4 | .3 | nil |
| 9-1-B' | 6.7 | 54.1 | 39.2 | 1 | 0 | 110 | 7.4 | .5 | nil |
| 9-1-C | 7.7 | 68.2 | 24.0 | 0 | 2 | 48 | 7.6 | .4 | nil |
| 10-2-B | 8.4 | 43.4 | 48.2 | 0 | 17 | 55 | 5.5 | .3 | nil |
| 10-2-B' | 8.9 | 26.6 | 64.5 | 0 | 5 | 94 | 6.7 | .2 | nil |
| 10-2-C | 4.7 | 41.3 | 54.0 | 0 | 2 | 82 | 6.2 | .2 | nil |
| 10-2-D | 5.7 | 42.9 | 51.4 | 0 | 2 | 32 | 6.5 | .1 | nil |
| 10-2-E | 11.0 | 24.0 | 65.0 | 0 | 2 | 102 | 6.5 | .1 | nil |
| 10-1-B | 6.3 | 41.3 | 52.4 | 1 | 5 | 55 | 6.3 | .2 | nil |
| 10-1-C | 7.3 | 42.0 | 50.6 | 0 | 0 | 40 | 6.2 | .1 | nil |
| 10-1-D | 12.2 | 18.9 | 68.9 | 0 | 10 | 82 | 7.6 | .2 | nil |
| 11-1-B | 12.8 | 36.5 | 49.9 | 1 | 7 | 114 | 4.6 | .3 | nil |
| 11-1-C | 7.4 | 52.8 | 39.8 | 0 | 2 | 226 | 6.8 | .3 | nil |
| 11-1-D | 18.0 | 31.6 | 50.5 | 0 | 0 | 62 | 7.4 | .6 | nil |
| 12-1-B | 7.2 | 25.8 | 67.0 | 0 | 12 | 114 | 7.5 | .4 | nil |
| 12-1-C | 22.7 | 35.7 | 41.6 | 0 | 5 | 126 | 6.3 | .5 | nil |
| 12-1-D | 19.4 | 19.6 | 61.0 | 0 | 2 | 106 | 7.2 | .3 | nil |
| 13-1-B | 10.0 | 47.1 | 43.0 | 0 | 2 | 70 | 6.8 | .4 | nil |
| 13-1-C | 6.0 | 64.4 | 29.6 | 0 | 2 | 110 | 7.4 | .3 | nil |
| 13-1-D | 10.8 | 39.4 | 49.8 | 0 | 2 | 137 | 7.4 | .3 | nil |
| 14-1-B | 7.8 | 46.9 | 45.3 | 1 | 7 | 86 | 5.5 | .3 | nil |
| 14-1-C | 8.2 | 50.4 | 41.3 | 0 | 5 | 94 | 5.9 | .2 | nil |
| 14-1-D | 7.3 | 46.8 | 45.9 | 0 | 0 | 137 | 6.8 | .3 | nil |
| 14-1-E | 23.5 | 30.9 | 45.6 | 1 | 2 | 110 | 6.9 | .3 | nil |
| 14-1-F | 11.8 | 28.2 | 60.0 | 0 | 4 | 192 | 7.4 | .4 | 1 |
| 15-1-B | 14.4 | 54.3 | 31.3 | 1 | 17 | | 5.0 | .3 | nil |
| 15-1-C | 9.0 | 45.1 | 49.9 | 1 | 5 | 219 | 5.5 | .3 | nil |
| 15-1-D | 6.0 | 48.1 | 45.9 | 0 | 5 | 133 | 6.2 | .2 | nil |
| 15-1-E | 14.4 | 21.3 | 64.3 | 0 | 5 | 126 | 6.6 | .2 | nil |
| 15-1-F | 15.0 | 29.5 | 55.5 | 0 | 5 | 133 | 7.3 | .3 | 4 |

| Plot No. | C | Texture Si | Sa | Pounds N | per P | acre K | Soil re- action (pH) | Conduc- tivity mmhos. | Free Lime CaCO ₃ |
|----------|------|------------|------|----------|-------|--------|----------------------|-----------------------|-----------------------------|
| 16-1-B | 5.4 | 31.0 | 63.6 | 0 | 19 | 161 | 6.2 | .3 | nil |
| 16-1-C | 3.9 | 46.6 | 49.6 | 0 | 12 | 230 | 6.7 | .1 | nil |
| 16-1-C' | 4.9 | 46.0 | 49.1 | 0 | 12 | 222 | 6.8 | .1 | nil |
| 16-1-D | 5.3 | 22.3 | 72.4 | 0 | 5 | 55 | 6.9 | .1 | nil |
| 16-1-D' | 3.3 | 19.8 | 76.9 | 0 | 5 | 52 | 6.9 | .1 | nil |
| 16-1-E | 9.5 | 25.8 | 64.9 | 0 | 7 | 74 | 7.1 | .2 | 1 |
| 16-1-E' | 3.8 | 12.8 | 83.3 | 0 | 2 | 74 | 7.4 | .4 | 7 |
| 16-1-E'' | 3.3 | 15.8 | 80.9 | 0 | 5 | 90 | 7.4 | .3 | nil |
| 16-1-F | 3.4 | 20.2 | 76.4 | 0 | 5 | 102 | 7.5 | .3 | 5 |
| 17-1-B | 7.2 | 34.4 | 58.4 | 0 | 7 | 141 | 5.3 | .3 | nil |
| 17-1-C | 6.6 | 39.3 | 54.1 | 0 | 5 | 78 | 6.3 | .3 | nil |
| 17-1-D | 5.4 | 7.4 | 87.2 | 0 | 5 | 48 | 6.0 | .2 | nil |
| 17-1-E | 4.4 | 3.7 | 91.9 | 0 | 7 | 32 | 6.5 | .1 | nil |
| 18-1-B | 7.1 | 29.8 | 63.1 | 0 | 15 | 196 | 5.5 | .3 | nil |
| 18-1-C | 8.2 | 29.2 | 62.6 | 0 | 22 | 207 | 5.7 | .3 | nil |
| 18-1-D | 17.6 | 33.1 | 49.3 | | | | | | |
| 19-1-B | 9.4 | 23.5 | 67.1 | 0 | 5 | 344 | 6.7 | .4 | nil |
| 19-1-C | 14.4 | 33.4 | 52.2 | 0 | 2 | 285 | 6.9 | .4 | nil |
| 19-1-D | 5.7 | 32.7 | 61.6 | 0 | 2 | 114 | 7.0 | .3 | nil |
| 19-1-E | 7.5 | 17.1 | 75.4 | 0 | 2 | 62 | 7.1 | .3 | nil |
| 20-1-B | 13.2 | 37.6 | 49.2 | 0 | 2 | 94 | 6.2 | .4 | nil |
| 20-1-C | 30.6 | 23.1 | 46.3 | 0 | 2 | 66 | 6.8 | .3 | nil |
| 21-1-B | 3.6 | 41.7 | 54.7 | 0 | 2 | 114 | 6.2 | .2 | nil |
| 21-1-C | 3.6 | 43.4 | 52.9 | 0 | 1 | 110 | 6.7 | .2 | nil |
| 21-1-D | 9.8 | 30.0 | 60.3 | 0 | 2 | 52 | 6.8 | .3 | nil |
| 22-1-B | 7.9 | 12.8 | 79.3 | 0 | 5 | 40 | 5.6 | .2 | nil |
| 22-1-C | 10.4 | 13.6 | 76.1 | 0 | 2 | 59 | 7.2 | .3 | 1 |
| 22-1-D | 4.3 | 12.6 | 83.1 | 0 | Tr | 20 | 7.6 | .4 | 4 |
| 22-2-B | 35.9 | 20.1 | 44.0 | 0 | 1 | 536 | 7.1 | .5 | nil |
| 22-2-C | 21.6 | 24.9 | 53.5 | 0 | 2 | 324 | 7.2 | .4 | nil |
| 23-1-B | 12.2 | 45.0 | 42.8 | 0 | 2 | 90 | 6.8 | .2 | nil |
| 23-1-C | 22.4 | 31.4 | 46.2 | 0 | Tr | 106 | 7.3 | .3 | nil |
| 23-1-D | 26.2 | 9.4 | 64.4 | 0 | Tr | 118 | 7.6 | .3 | 4 |
| 24-1-B | 9.6 | 39.4 | 51.0 | 0 | 5 | 285 | 6.7 | .2 | nil |
| 24-1-C | 7.7 | 29.2 | 63.1 | 0 | 7 | 145 | 6.7 | .1 | nil |
| 24-1-D | 6.6 | 10.0 | 83.3 | 0 | 2 | 90 | 7.0 | .1 | nil |
| 24-1-E | 2.7 | 6.4 | 90.9 | 0 | 5 | 137 | 7.5 | .3 | 3 |
| 24-1-F | 9.6 | 14.1 | 76.3 | 0 | 1 | 66 | 7.8 | .3 | 6 |
| 25-1-B | 4.7 | 14.6 | 80.7 | 0 | Tr | 36 | 6.0 | .1 | nil |
| 25-1-C | 5.1 | 25.2 | 69.7 | 0 | 2 | 20 | 6.4 | .07 | nil |

| Plot No. | C | Texture Si | Sa | Pounds N | per P | acre K | Soil re- action (pH) | Conduc- tivity mmhos. | Free Lime CaCO ₃ |
|----------|------|------------|------|----------|-------|--------|----------------------|-----------------------|-----------------------------|
| 26-1-B | 8.5 | 52.2 | 39.3 | 0 | 5 | 70 | 5.4 | .2 | nil |
| 26-1-C | 6.9 | 48.2 | 44.9 | 0 | 0 | 90 | 6.6 | .1 | nil |
| 26-1-C' | 11.3 | 43.0 | 45.7 | 0 | 2 | 40 | 6.4 | .1 | nil |
| 26-1-D | 6.8 | 22.0 | 71.2 | 0 | 2 | 44 | 6.4 | .1 | nil |
| 27-1-B | 5.0 | 29.3 | 65.7 | 0 | 2 | 122 | 6.7 | .2 | nil |
| 27-1-C | 3.8 | 12.9 | 83.3 | 0 | 5 | 70 | 6.8 | .1 | nil |
| 27-1-D | 4.5 | 9.3 | 86.2 | 0 | 2 | 28 | 7.7 | .2 | 5 |
| 28-1-B | 4.6 | 37.2 | 58.3 | 0 | 0 | 48 | 6.5 | .1 | nil |
| 28-1-C | 5.0 | 13.9 | 81.1 | 0 | 2 | 24 | 6.3 | .07 | nil |
| 28-1-D | 5.5 | 11.4 | 83.1 | 0 | 2 | 20 | 6.4 | .07 | nil |
| 28-1-E | 19.0 | 22.4 | 58.6 | 0 | 0 | 94 | 7.5 | .3 | 4 |
| 29-1-B | 6.1 | 44.7 | 49.2 | 0 | 1 | 118 | 6.2 | .1 | nil |
| 29-1-C | 13.8 | 22.4 | 63.8 | 0 | 2 | 82 | 7.4 | .3 | nil |
| 30-1-B | 5.3 | 34.7 | 60.0 | 0 | 2 | 70 | 6.8 | .1 | nil |
| 30-1-C | 4.8 | 22.2 | 73.0 | 0 | 2 | 16 | 6.8 | .1 | nil |
| 30-1-D | 17.0 | 21.2 | 61.8 | 0 | 1 | 110 | 7.3 | .5 | 3 |
| 31-1-B | 8.9 | 50.0 | 41.1 | 0 | 4 | 48 | 5.3 | .2 | nil |
| 31-1-C | 5.0 | 40.7 | 54.2 | 0 | 0 | 82 | 6.4 | .1 | nil |
| 31-1-D | 18.0 | 25.5 | 56.5 | 0 | Tr | 94 | 7.0 | .3 | 1 |
| 31-2-B | 5.0 | 51.9 | 43.1 | 0 | 0 | 66 | 6.6 | .2 | nil |
| 31-2-C | 15.6 | 25.8 | 58.4 | 0 | 0 | 66 | 7.4 | .3 | 1 |
| 32-2-B | 5.7 | 39.0 | 55.3 | 0 | 2 | 183 | 6.6 | .2 | nil |
| 32-2-B' | 5.8 | 49.4 | 44.9 | 0 | 4 | 110 | 6.9 | .2 | nil |
| 32-2-C | 4.2 | 16.5 | 79.3 | 0 | 5 | 118 | 7.3 | .4 | 1 |
| 33-1-B | 10.8 | 42.4 | 46.8 | 1 | 7 | 122 | 5.8 | .4 | nil |
| 33-1-C | 12.9 | 30.0 | 37.1 | 0 | 2 | 145 | 7.1 | .3 | nil |
| 33-1-D | 9.8 | 10.3 | 79.8 | 0 | 2 | 126 | 7.2 | .3 | nil |
| 33-1-E | 18.9 | 24.9 | 56.3 | 0 | 2 | 59 | 7.8 | .4 | 6 |
| 34-1-B | 5.9 | 40.2 | 53.8 | 0 | 2 | 62 | 7.4 | .3 | nil |
| 34-1-B' | 15.1 | 39.6 | 45.3 | 0 | 2 | 161 | 7.6 | .4 | 1 |
| 34-1-C | 12.8 | 20.0 | 67.1 | 0 | 5 | 102 | 7.3 | .3 | nil |
| 34-1-C | 25.9 | 28.1 | 46.1 | 0 | 2 | 102 | 7.8 | .3 | 8 |
| 35-1-B | 6.0 | 53.3 | 40.7 | 0 | 2 | 62 | 6.6 | .3 | nil |
| 35-1-C | 10.0 | 18.4 | 71.6 | 0 | 12 | 78 | 7.2 | .3 | 1 |
| 36-1-B | 10.7 | 35.2 | 44.0 | 0 | 7 | 98 | 5.0 | .4 | nil |
| 36-1-C | 28.5 | 20.8 | 50.8 | 0 | 2 | 133 | 7.1 | .4 | nil |
| 36-1-D | 19.4 | 24.2 | 56.4 | 0 | Tr | 52 | 7.9 | .4 | 5 |
| 36-1-E | 28.0 | 25.1 | 47.0 | 0 | 0 | 62 | 7.9 | .4 | 5 |

| Plot No. | C | Texture Si | Sa | Pounds per acre | | | Soil re- action (pH) | Conduc- tivity mmhos. | Free Lime CaCO ₃ |
|-------------|------|---------------|------|-----------------|----|-----|----------------------------|-----------------------------|-----------------------------------|
| 37-1-B | 14.4 | 19.1 | 66.5 | 0 | 10 | 59 | 6.7 | .3 | nil |
| 37-1-C | 14.1 | 17.9 | 68.1 | 0 | 15 | 66 | 7.0 | .4 | nil |
| 39-1-B | 12.7 | 51.7 | 35.5 | 0 | 15 | 94 | 6.8 | .3 | nil |
| 39-2-B | | | | 0 | 10 | 78 | 4.8 | .2 | 3 |
| 39-1-C | 18.6 | 30.4 | 51.0 | 0 | 2 | 86 | 7.3 | .3 | 4 |
| 40-1-E | 5.5 | 35.9 | 58.5 | 0 | 2 | 55 | 7.8 | .3 | 5 |
| 40-1-B | 11.1 | 50.3 | 38.6 | 0 | 5 | 40 | 5.8 | .2 | nil |
| 40-1-C | 11.9 | 43.2 | 44.9 | 0 | 2 | 40 | 6.5 | .2 | nil |
| 40-1-D | 5.0 | 16.4 | 78.6 | 0 | 2 | 28 | 7.0 | .2 | nil |
| 41-1-C | 11.5 | 35.4 | 53.1 | 0 | 2 | 94 | 6.0 | .2 | nil |
| 41-1-D | | | | 0 | 12 | 74 | 5.7 | .1 | nil |
| 42-1-B | 9.1 | 15.1 | 75.8 | 0 | 5 | 70 | 4.7 | .1 | nil |
| 42-1-C | 8.6 | 4.4 | 87.0 | 0 | 10 | 36 | 6.6 | .1 | nil |
| 42-1-D | 3.0 | 4.5 | 92.5 | 0 | 2 | 12 | 7.2 | .2 | 3 |
| 43-1-B | 22.5 | 31.3 | 46.2 | 1 | 2 | 129 | 6.9 | .4 | 1 |
| 43-1-C | 15.3 | 16.4 | 68.3 | 0 | 2 | 44 | 7.5 | .4 | nil |
| 43-1-D | 18.8 | 21.4 | 59.9 | 0 | 1 | 48 | 7.8 | .4 | 5 |
| 44-1-B | 27.6 | 28.8 | 43.6 | 0 | 5 | 102 | 6.5 | .3 | nil |
| 44-1-C | 12.3 | 17.9 | 69.8 | 0 | 2 | 48 | 7.5 | .4 | 5 |
| 45-1-B | 6.9 | 40.3 | 52.8 | 0 | 1 | 70 | 7.0 | .2 | nil |
| 45-1-C | 8.7 | 7.6 | 83.7 | 0 | 2 | 74 | 7.3 | .4 | nil |
| 45-1-D | 22.4 | 25.5 | 52.1 | 0 | 2 | 70 | 8.0 | .3 | 6 |
| 46-1-B | 18.2 | 39.3 | 42.5 | 0 | 4 | 211 | 7.4 | .4 | nil |
| 46-1-C | 18.8 | 27.8 | 53.4 | 0 | 1 | 90 | 7.7 | .4 | 5 |
| 46-1-D | 24.3 | 26.1 | 49.6 | 0 | 1 | 52 | 8.1 | .3 | 6 |
| 47-1-B | 10.0 | 36.0 | 54.0 | 0 | 5 | 62 | 7.3 | .2 | nil |
| 47-1-C | 7.8 | 17.2 | 75.0 | 0 | 5 | 48 | 7.6 | .3 | 5 |
| 48-1-B | 7.9 | 47.5 | 44.6 | 0 | 7 | 180 | 6.9 | .3 | 1 |
| 48-1-C | 16.3 | 30.9 | 52.8 | 0 | 10 | 126 | 7.1 | .3 | nil |
| 48-1-D | 12.2 | 32.1 | 55.7 | 0 | 15 | 106 | 7.6 | .4 | 4 |
| 49-1-B | 10.4 | 25.2 | 64.4 | 0 | 2 | 55 | 7.7 | .3 | 3 |
| 49-1-C | 12.8 | 39.6 | 47.5 | 0 | 2 | 40 | 8.1 | .3 | 8 |
| 50-1-B | 4.4 | 24.5 | 71.1 | 5 | 4 | 94 | 7.6 | .5 | 7 |
| 50-1-C | 10.0 | 45.0 | 44.9 | 0 | 0 | 176 | 7.9 | .4 | 4 |
| 50-1-D | 8.4 | 25.9 | 65.7 | 0 | 0 | 48 | 7.9 | .4 | 8 |
| 50-1-E | 12.9 | 16.6 | 70.5 | 0 | 0 | 20 | 8.0 | .3 | 8 |

| Plot No. | C | Texture Si | Sa | Pounds N | per P | acre K | Soil re- action (pH) | Conduc- tivity mmhos. | Free Lime CaCO ₃ |
|---------------------|------|------------|------|----------|-------|--------|----------------------|-----------------------|-----------------------------|
| 51-1-B | 14.8 | 53.6 | 31.6 | 0 | 7 | 90 | 5.6 | .3 | 2 |
| 51-1-C | 14.7 | 42.0 | 43.3 | 0 | 1 | 149 | 7.0 | .4 | 1 |
| 52-1-B | 5.9 | 25.2 | 68.9 | 0 | 2 | 40 | 6.0 | .2 | nil |
| 52-1-C | 5.3 | 4.7 | 90.0 | 0 | 2 | 24 | 6.5 | .1 | nil |
| 52-1-D | 7.9 | 5.6 | 86.4 | 0 | 2 | 40 | 7.0 | .4 | 2 |
| 53-1-B | 6.5 | 30.0 | 63.5 | 0 | 2 | 78 | 6.1 | .3 | nil |
| 53-1-C | 10.4 | 20.7 | 68.9 | 0 | 2 | 24 | 6.5 | .1 | nil |
| 53-1-D | 22.5 | 19.7 | 57.8 | 0 | 2 | 66 | 7.5 | .3 | 4 |
| 54-1-B | 5.5 | 40.1 | 54.4 | 0 | Tr | 172 | 7.3 | .3 | nil |
| 54-1-C | 22.2 | 27.4 | 50.3 | 0 | 0 | 168 | 7.9 | .3 | 3 |
| 54-1-D | 14.5 | 30.6 | 54.9 | 0 | 0 | 52 | 8.0 | .3 | 5 |
| 55-1-B | 9.2 | 37.0 | 53.8 | 0 | Tr | 118 | 7.1 | .3 | nil |
| 55-1-C | 14.1 | 21.1 | 64.9 | 0 | 1 | 59 | 7.3 | .3 | 1 |
| 56-1-B | 7.2 | 38.8 | 54.0 | 0 | 4 | 62 | 6.7 | .3 | nil |
| 56-1-C | 13.3 | 20.6 | 66.1 | 0 | 5 | 126 | 6.8 | .4 | 1 |
| 56-1-D | 5.2 | 6.0 | 88.8 | 0 | 5 | 36 | 7.4 | .3 | 4 |
| 57-1-B | 12.0 | 48.2 | 39.8 | 0 | 2 | 141 | 7.3 | .3 | 1 |
| 57-1-C | 8.8 | 20.7 | 70.6 | 0 | 0 | 48 | 7.5 | .4 | 5 |
| 57-1-D | 11.2 | 18.0 | 70.8 | 0 | 2 | 36 | 7.6 | .3 | 8 |
| 58-1-B | 9.3 | 20.0 | 70.7 | 0 | 5 | 48 | 6.5 | .1 | nil |
| 58-1-C | 44.2 | 21.7 | 34.1 | 0 | 5 | 141 | 6.2 | .2 | nil |
| 58-1-D | 21.9 | 18.3 | 59.8 | 0 | 2 | 74 | 6.5 | .7 | nil |
| 59-1-B | 11.8 | 60.3 | 27.9 | 0 | 10 | 32 | 5.3 | .1 | nil |
| 59-1-C | 9.1 | 45.9 | 45.0 | 0 | 2 | 74 | 6.5 | .2 | 1 |
| 59-1-D | | | | 0 | 5 | 149 | 5.7 | .2 | 1 |
| 59-1-E | 8.7 | 7.1 | 84.3 | 0 | 5 | 110 | 7.2 | .3 | 5 |
| 60-1-B | 11.8 | 57.7 | 30.5 | 0 | 43 | 36 | 4.9 | .1 | nil |
| 60-1-B' | 10.0 | 39.4 | 50.6 | 0 | 5 | 62 | 5.9 | .1 | nil |
| 60-1-C | 9.5 | 20.8 | 69.7 | 0 | 38 | 122 | 5.7 | .2 | nil |
| 60-1-D | 4.8 | 10.7 | 84.5 | 0 | 10 | 94 | 7.2 | .3 | 3 |
| 61-1-B | | | | 0 | 5 | 32 | 6.6 | .4 | nil |
| 61-1-C | 8.5 | 39.1 | 52.4 | 0 | 2 | 32 | 6.1 | .2 | nil |
| M ₃ -1-B | 12.7 | 47.3 | 40.0 | 0 | 191 | 214 | 6.2 | .3 | nil |
| M ₃ -1-C | 11.2 | 32.6 | 56.2 | 0 | 50 | 133 | 6.6 | .3 | nil |
| M ₄ -1-B | 7.1 | 68.3 | 24.6 | 0 | 5 | 44 | 6.3 | .1 | nil |
| M ₄ -1-C | 19.3 | 26.9 | 57.8 | 0 | 22 | 129 | 6.6 | .1 | nil |
| M ₄ -1-D | 17.3 | 29.0 | 53.8 | 0 | 24 | 161 | 7.5 | .3 | nil |

| Plot No. | C | Texture Si | Sa | Pounds N | per P | acre K | Soil re- action (pH) | Conduc- tivity mmhos. | Free Lime CaCO ₃ |
|-------------|------|---------------|------|-------------|----------|-----------|----------------------------|-----------------------------|-----------------------------------|
| 62-1-B | 17.3 | 38.5 | 44.2 | 0 | 10 | 141 | 6.6 | .1 | nil |
| 62-1-C | 21.2 | 29.4 | 49.4 | 1 | 7 | 211 | 6.9 | .4 | 1 |
| 62-1-D | 6.2 | 32.5 | 61.3 | 0 | 2 | 44 | 7.2 | .4 | 5 |
| 62-1-E | 20.4 | 48.4 | 31.2 | 0 | 2 | 36 | 7.6 | .4 | 6 |
| 63-1-B | 15.8 | 42.3 | 41.9 | 0 | 5 | 110 | 7.2 | .3 | nil |
| 63-1-C | 15.7 | 22.5 | 61.8 | 0 | 2 | 48 | 7.6 | .3 | 6 |
| 24-I-1 | 7.7 | 33.6 | 58.7 | 0 | 7 | 180 | 6.8 | .3 | nil |
| 24-I-2 | 9.3 | 20.8 | 70.0 | 0 | 17 | 86 | 6.6 | .2 | nil |
| 24-I-3 | 10.9 | 9.7 | 79.5 | 0 | 24 | 145 | 7.2 | .3 | nil |
| 24-I-4 | 9.3 | 5.6 | 85.1 | 0 | 15 | 129 | 7.4 | .2 | 4 |
| 26-I-B | 12.2 | 47.6 | 40.2 | 0 | 2 | 70 | 6.5 | .1 | nil |
| 26-I-C | 20.9 | 32.4 | 46.7 | 0 | 5 | 62 | 7.6 | .2 | nil |
| 26-I-E | 10.3 | 4.5 | 85.2 | 0 | 2 | 44 | 7.4 | .1 | 3 |
| 41-I-B | 11.6 | 44.2 | 44.2 | 0 | 10 | 55 | 4.5 | .1 | nil |
| 41-I-C | 8.0 | 46.2 | 45.9 | 0 | 2 | 78 | 6.4 | .1 | nil |
| 41-I-D | 7.8 | 8.0 | 84.1 | 0 | 5 | 59 | 5.6 | .1 | nil |
| 41-I-E | 19.9 | 22.1 | 58.0 | 0 | 2 | 62 | 6.3 | .2 | nil |
| 41-I-F | 10.3 | 14.6 | 75.1 | 0 | 4 | 52 | 6.5 | .2 | nil |
| 47-I-B | 12.7 | 33.3 | 54.0 | 0 | 12 | 32 | 4.9 | .1 | nil |
| 47-I-C | 10.5 | 31.0 | 58.5 | 0 | 2 | 70 | 5.5 | .1 | nil |
| 47-I-D | 5.1 | 4.1 | 90.8 | 1 | 2 | 28 | 7.2 | .2 | 6 |
| 47-I-E | 5.8 | 19.8 | 74.4 | 0 | Tr | 36 | 7.4 | .3 | 5 |
| 47-I-F | 3.8 | 3.2 | 93.0 | 0 | 1 | 24 | 7.5 | .2 | 4 |
| 55-I-B | 7.9 | 52.1 | 40.0 | 0 | 0 | 55 | 6.6 | .1 | nil |
| 55-I-C | 9.9 | 50.0 | 40.0 | 0 | 2 | 94 | 6.8 | .3 | 1 |
| 55-I-D | 21.0 | 20.3 | 58.7 | 0 | 2 | 66 | 7.3 | .3 | 5 |

2. MECHANICAL SOIL ANALYSIS

1. 100 g of air-dry soil (less than 2 mm portion) were placed in a 500 ml flask to which was added 10 ml of 5% Calgon (sodium hexametaphosphate) and approximately 400 ml of water.
2. The flasks were sealed, shaken for one hour in a reciprocal shaker, allowed to slake for 23 hours, then shaken for one hour. The contents of the flasks were then emptied into sedimentation cylinders to which was added enough water to bring the volume to 1000 mls.
3. The cylinders were then manually shaken for 35 seconds. After 40 seconds of settling, the first hydrometer and temperature readings were taken. The 40 second readings were repeated and a difference of not more than $\frac{1}{2}$ unit of the hydrometer was deemed acceptable or else a repeat reading was required. The next readings were made at two hours.
4. A 25 gm air-dry sample of each soil was oven dried at 105° C. to determine the amount of water present. The amount of water present in the 100 gm air-dry sample analyzed was estimated from this subsample and the calculations of % sand, % silt, and % clay were based upon the corrected oven dry weight.

3. MODIFICATION OF REAM'S FORTRAN IV COMPUTER PROGRAM FOR CALCULATING INDICES OF SIMILARITY

The program available at the Plant Ecology Laboratory, Department of Botany, University of Alberta, still calculates the index $2w/(a+b)$, but modifications by J. Purchase and R. Hnatiuk have been made. These are:

1. an "echo check" of data is possible;
2. the inverse data matrix may be read into the program;
3. the indices may be written out on:
 - (a) line printer
 - (b) cards
 - (c) unit "8"

(the last type of out-put allows Ream's program to be linked to other programs such as "sort-merge" and cluster analysis.

4. both similarities and dissimilarities may be calculated.

4. AERIAL PHOTOGRAPH LOCATION OF INTENSIVE STANDS

The aerial photographs were divided into four quadrants with the origin at the marked centre of the photograph. The coordinates of points marking the location of the Intensive Stands are given as centimeters from the origin (positive if to the right and top, and negative if to the left and bottom of photo). The coordinates of the E-W (horizontal) line are given first then the N-S (vertical) line coordinates next.

| Stand | E-W Line | N-S Line | Photograph No. |
|--------|----------|----------|------------------------|
| 41-B-I | 5.5 | -1.2 | 160-5112X 2424 - 87 |
| 47-B-I | -0.9 | 4.3 | 160-5021X 2278 - 71 |
| 26-J-I | -3.9 | -5.6 | 160-5217X 1472 - 11 |
| 55-J-I | -6.5 | 2.5 | 160-5213X 1473 - 14 |
| 24-J-I | 7.0-7.5 | 1.5-2.0 | 160-5218X 1472 - 11 |

5. PRESENCE LIST OF BRYOPHYTES AND LICHENS (from 6 stands)

| species | stands | 24 | 26 | 37 | 41 | 47 | 55 |
|---------------------------------|--------|----|----|----|----|----|----|
| <i>Aulacomium palustre</i> | | p | p | . | . | . | . |
| <i>Brachythecium salebrosum</i> | | p | | | p | p | p |
| <i>Ceratodon purpureus</i> | | . | : | : | p | . | . |
| <i>Dicranum fuscescens</i> | | . | p | . | p | p | p |
| <i>Dicranum polysetum</i> | | p | p | p | p | p | . |
| <i>Dicranum scoparium</i> | | p | p | p | p | p | . |
| <i>Drepanocladus uncinatus</i> | | ? | . | p | p | p | . |
| <i>Eurhynchium pulchellum</i> | | p | p | . | . | . | . |
| <i>Hylocomium splendens</i> | | p | p | p | p | p | p |
| <i>Orthocaulus</i> sp. | | . | ? | p | . | . | . |

| species | stands | 24 | 26 | 37 | 41 | 47 | 55 |
|--|--------|----|----|----|----|----|----|
| <i>Pleurozium schreberi</i> | | p | p | p | p | p | p |
| <i>Pohlia nutans</i> | | p | p | p | p | p | p |
| <i>Polytrichum commune</i> | | . | . | . | p | . | . |
| <i>Polytrichum juniperinum</i> | | . | p | . | p | p | p |
| <i>Polytrichum piliferum</i> | | . | . | p | . | p | . |
| <i>Ptilium crista-castrensis</i> | | p | p | p | p | p | p |
| <i>Racomitrium canescens</i> | | . | . | . | . | . | p |
| <i>Rhytidiadelphus triquetrus</i> | | . | . | . | . | . | p |
| <i>Rhytidiadelphus loreus</i> | | . | . | . | . | p | . |
| <i>Splachnum ovatum</i> | | . | . | . | p | . | . |
| <i>Tetraplodon angustatus</i> | | . | . | p | . | . | . |
| <i>Barbilophozia hatcheri</i> | | . | p | p | p | p | . |
| <i>Lophozia ventricosa</i> | | . | . | . | p | . | . |
| <i>Ptilidium pulcherrimum</i> | | p | p | . | p | p | p |
| <i>Alectoria americana</i> | | . | p | p | . | . | . |
| <i>Alectoria glabra</i> | | p | . | p | . | . | . |
| <i>Alectoria sarmentosa</i> | | . | . | p | . | . | . |
| <i>Buellia triphragmiodes</i> | | . | p | . | . | . | . |
| <i>Blastenia sinapisperma</i> | | . | . | p | . | . | . |
| <i>Calicium microcephallum</i> | | . | . | p | . | . | . |
| <i>Caloplaca holocarpa</i> | | p | . | . | . | . | . |
| <i>Cetraria cucullata</i> | | p | . | . | . | . | . |
| <i>Cetraria ericetorum</i> | | p | p | p | . | p | . |
| <i>Cetraria merrilli</i> | | p | . | . | p | . | . |
| <i>Cetraria nivalis</i> | | . | . | p | . | . | . |
| <i>Cetraria pinastri</i> | | p | p | p | p | . | . |
| <i>Cetraria scutata</i> | | . | p? | p | . | . | . |
| <i>Cladonia bacillaris</i> | | . | . | . | . | p | . |
| <i>Cladonia cariosa</i> | | . | . | p | . | . | . |
| <i>Cladonia cenotea</i> | | . | p | p | p | p | p |
| <i>Cladonia chlorophaea</i> | | . | p | . | . | . | . |
| <i>Cladonia coccifera</i> | | . | p | p | . | . | . |
| <i>Cladonia coniocraea</i> | | p | . | . | . | . | . |
| <i>Cladonia cornuta f. cylindrica</i> | | . | p | p | . | p | . |
| <i>Cladonia crispata</i> | | p | p | . | . | . | . |
| <i>Cladonia cylindrica</i> | | p | p | ? | . | p | . |
| <i>Cladonia deformis</i> | | . | . | p | p | . | . |
| <i>Cladonia ecmocyna</i> | | . | p | p | p | p | p |
| <i>Cladonia furcata</i> | | . | . | p | . | p | . |
| <i>Cladonia gracilis var. dilatata</i> | | p | p | p | . | . | . |
| <i>Cladonia gonecha</i> | | p | . | . | . | p | . |
| <i>Cladonia mitis</i> | | p | p | p | . | . | p |
| <i>Cladonia multiformis</i> | | p | p | . | . | . | p |
| <i>Cladonia nemosyna</i> | | . | p | p | . | . | . |
| <i>Cladonia phyllophora</i> | | . | p | . | . | . | . |
| <i>Cladonia pleurota</i> | | . | . | . | . | . | p |
| <i>Cladonia pyxidata</i> | | p | p | p | . | . | p |
| <i>Cladonia rangiferina</i> | | . | p | . | . | . | . |

| species | stands | 24 | 26 | 37 | 41 | 47 | 55 |
|--|--------|----|----|----|----|----|----|
| <i>Hypogymnia austerodes</i> | | p | . | p | p | . | . |
| <i>Hypogymnia physodes</i> | | p | p | . | . | . | . |
| <i>Hypogymnia vittata</i> | | p | . | p | p | . | . |
| <i>Icmadophila ericetorum</i> | | . | . | . | p | p | . |
| <i>Letharia vulpina</i> | | p | p | p | p | . | . |
| <i>Parmelia exasperatula</i> | | . | . | . | . | . | p |
| <i>Parmelia sulcata</i> | | p | . | p | . | . | . |
| <i>Parmeliopsis ambigua</i> | | p | p | p | . | . | . |
| <i>Parmeliopsis hyperota</i> | | p | p | p | p | . | . |
| <i>Peltigera aphthosa</i> var. <i>aphthosa</i> | | . | p | . | p | p | . |
| <i>Peltigera canina</i> var. <i>canina</i> | | . | p | . | p | p | . |
| <i>Peltigera canina</i> var. <i>rufescens</i> | | . | p | p | p | . | p |
| <i>Peltigera canina</i> var. <i>spongiosa</i> | | . | . | p | . | . | . |
| <i>Peltigera malacea</i> | | p | p | p | . | . | . |
| <i>Peltigera polydactyla</i> | | p | . | . | . | . | . |
| <i>Peltigera pulverulenta</i> | | p | . | . | . | . | . |
| <i>Peltigera venosa</i> | | . | . | . | p | . | p |
| <i>Psoroma hypnorum</i> | | . | p | p | . | . | . |
| <i>Solorina crocea</i> | | . | . | . | p | . | . |
| <i>Stereocaulon tomentosum</i> | | p | p | p | p | p | p |
| <i>Usnea glabrescens</i> | | p | . | p | . | p | . |
| <i>Usnea hirta</i> | | . | p | . | . | . | . |
| <i>Usnea scabrata</i> spp. <i>nylanderiana</i> | | . | . | . | p | . | . |
| <i>Usnea sorediifera</i> var. <i>substerilis</i> | | p | . | . | . | . | . |

The species in this list are not intended to represent the complete bryophyte-lichen flora for the pine vegetation, rather they give some idea of the diversity of commoner taxa. Such diversity alone indicates the need for more detailed studies of the role of these plants in the vegetation.

[illegible]

| | | | | |
|-----|-----|-----|-----|-----|
| 10 | 11 | 12 | 13 | 14 |
| 15 | 16 | 17 | 18 | 19 |
| 20 | 21 | 22 | 23 | 24 |
| 25 | 26 | 27 | 28 | 29 |
| 30 | 31 | 32 | 33 | 34 |
| 35 | 36 | 37 | 38 | 39 |
| 40 | 41 | 42 | 43 | 44 |
| 45 | 46 | 47 | 48 | 49 |
| 50 | 51 | 52 | 53 | 54 |
| 55 | 56 | 57 | 58 | 59 |
| 60 | 61 | 62 | 63 | 64 |
| 65 | 66 | 67 | 68 | 69 |
| 70 | 71 | 72 | 73 | 74 |
| 75 | 76 | 77 | 78 | 79 |
| 80 | 81 | 82 | 83 | 84 |
| 85 | 86 | 87 | 88 | 89 |
| 90 | 91 | 92 | 93 | 94 |
| 95 | 96 | 97 | 98 | 99 |
| 100 | 101 | 102 | 103 | 104 |

The first part of the document is a list of names and their corresponding numbers. The names are written in a cursive script, and the numbers are in a standard font. The list is organized in a table-like format with five columns.

The second part of the document is a list of names and their corresponding numbers. The names are written in a cursive script, and the numbers are in a standard font. The list is organized in a table-like format with five columns.

The third part of the document is a list of names and their corresponding numbers. The names are written in a cursive script, and the numbers are in a standard font. The list is organized in a table-like format with five columns.

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The fifth part of the document is a list of names and their corresponding numbers. The names are written in a cursive script, and the numbers are in a standard font. The list is organized in a table-like format with five columns.

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

| | | | | | |
|-----|-----|-----|-----|-----|-----|
| 10 | 11 | 12 | 13 | 14 | 15 |
| 16 | 17 | 18 | 19 | 20 | 21 |
| 22 | 23 | 24 | 25 | 26 | 27 |
| 28 | 29 | 30 | 31 | 32 | 33 |
| 34 | 35 | 36 | 37 | 38 | 39 |
| 40 | 41 | 42 | 43 | 44 | 45 |
| 46 | 47 | 48 | 49 | 50 | 51 |
| 52 | 53 | 54 | 55 | 56 | 57 |
| 58 | 59 | 60 | 61 | 62 | 63 |
| 64 | 65 | 66 | 67 | 68 | 69 |
| 70 | 71 | 72 | 73 | 74 | 75 |
| 76 | 77 | 78 | 79 | 80 | 81 |
| 82 | 83 | 84 | 85 | 86 | 87 |
| 88 | 89 | 90 | 91 | 92 | 93 |
| 94 | 95 | 96 | 97 | 98 | 99 |
| 100 | 101 | 102 | 103 | 104 | 105 |

The following is a list of the names of the persons who have been elected to the office of Justice of the Peace for the year 1900. The names are given in alphabetical order of their surnames.

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APPENDIX 7. INDICES OF SIMILARITY BETWEEN STANDS OF PRIMARY SURVEY

[illegible]

PLATE IV.
1891.

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